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STUDIES ON THE BIOLOGY AND CONTROL OF THE LARCH SAWFLY

IN NORTHERN MINNESOTA - 1950

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By

James W. Butcher

Forest Insect Laboratory
628 E. Michigan Street
Milwaukee 2, Wisconsin

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PROGRESS REPORT

STUDIES ON THE BIOLOGY AND CONTROL OF THE LARCH SAWFLY IN NORTHERN MINNESOTA - 1950 1/

INTRODUCTION

The literature contains numerous records of outbreaks of the larch sawfly (Pristiphora erichsonii (Htg.)) which occurred in North America during the 19th and 20th Centuries, but the consequences of heavy attack in terms of tree mortality are not clearly stated. When it became evident in 1948 that this insect was once again on the increase, it was apparent that too little was known about its biology and its potentiality for destruction to permit establishment of an intelligent and realistic basis for control.

Old reports of tamarack mortality caused by this species made it imperative that the magnitude of the current epidemic be rapidly assessed and that immediate research be initiated in order to evaluate direct control methods which were developed since the last outbreak had run its course. Further, it seemed desirable to obtain concrete evidence of the destructive capabilities of this insect, since tamarack (Larix laricina (du Roi) Koch), a deciduous conifer, was known for its ability to survive one or more successive defoliations without discernible injury (Graham, 1931; Craighead, 1940).

It was toward fulfillment of these objectives that most of the 1949 and 1950 field seasons were devoted by the writer and several technicians assigned to the problem. As a consequence of this work, by 1950 it was possible to depict the limits of the outbreak and tabulate with some degree of accuracy the acreages involved. Also, by the end of 1950, useful information on ecology of the insect and the host species had been accumulated which promised to permit a more intelligent approach to control by chemical and cultural or management procedures. This paper purports to detail the course of these investigations and evaluate the usefulness of their results in terms of a practical approach to control. Definitive recommendations must await the results of closely allied research currently in progress in Canada (chiefly at the Dominion Forest Insect Laboratory in Winnipeg, Manitoba), as well as projected investigations to be carried out in the United States.

1/ The investigations reported here were carried out by the Forest Insect Laboratory, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, located at Milwaukee, Wisconsin in cooperation with the Division of Entomology and Economic Zoology of the University of Minnesota, the U. S. Forest Service, the Minnesota Department of Conservation, Division of Forestry and the St. Louis County Land Commissioner's Office.

The material contained in this report represents in part the results of work carried out in 1950 by the writer. Assistance with these and other phases of the 1950 work program was supplied by two Field Aids, James C. Feigal and Stanley A. Gruetzman.

Historical Review of Outbreaks in North America

Reports of epidemics of the larch sawfly are numerous and of questionable accuracy. As early as 1881 (Hagen, 1881) the insect was recorded from Massachusetts. Jack (1887) states that he had seen the insect and that his father had recorded that tamarack was entirely defoliated as much as 30 years previously. Swaine (1933) and others suggest that the insect is probably European and was brought to this country more than 100 years previously. Graham (1929), on the other hand, estimates from studies of ring growth that the insect had been present in this country for at least a century prior to date of his publication, and that it very likely was indigenous.

Uncertainties as to its origin notwithstanding, there is ample testimony in the literature of the defoliation and injury caused by the sawfly in past years. Most reports of past epidemics are fragmentary and of such a nature as to make generalizations difficult. Swaine (1933) and Thielmann (1938) attempted to sum up these reports from the literature with the following results. The latter authority states that in the years immediately following 1880 a tremendous outbreak occurred extending throughout all Eastern Canada and the New England States from Nova Scotia and Maine to the Great Lakes. By 1890 nearly all larch of commercial size in Eastern Canada had died as a result of these attacks. Thielmann (1938) declares that the first great outbreak occurred in Minnesota about 1909, and in 1914-1915 the insect was epidemic in Quebec, Ontario and the western part of Saskatchewan. Beeson (1918) states that since 1880 this insect killed off 50 to 100 percent of all mature larch in Canada and the United States. Graham and Ruggles (1923) estimated that losses due to the larch sawfly and the spruce budworm in North America amounted to at least 60 million pounds sterling during the period 1905 to 1925.

In view of this history of destruction, it was not surprising in 1949 that land management agencies throughout the Lake States were concerned at reports of heavy defoliation by the sawfly which had come in during the last decade. Resurgence of the larch sawfly apparently began as early as 1940 in Minnesota (Hodson, 1940). Occurrence of the insect was more common in 1941 (Hodson and Christensen, 1941) but was reported less frequently through 1943 (Hodson and Christensen, 1943). In 1944-1945 heavy defoliation was observed at Pencer, along with a concomitant general increase at many points on the Chippewa (Hodson and Christensen, 1945). By 1947 (Hodson and Christensen, 1947) moderate to heavy infestations were described on the Chippewa and Superior National Forests, as well as at other points within the State. By 1948 the epidemic was threatening enough to encourage participation by the Minnesota Department of Conservation, the U. S. Forest Service and the Forest Insect Laboratory in a joint experimental aerial spraying operation at Cass Lake, Minnesota. Since that time the outbreak has continued to increase (Butcher, 1950; Butcher and Eaton, 1950).

Taxonomy and Biology

The larch sawfly, Pristiphora erichsonii, was described by Hartig (1837) under the generic name Nematus. The chaotic condition of the sub-family Nematinae (Ross, 1937) resulted in confusion whereby the insect was variously designated Lygaeonematus erichsonii (Marlatt, 1896) and Pristiphora erichsonii (Ross, 1937). The work of Ross (1937) incorporates the genus Lygaeonematus of Knnow (1890) into the sub-genus Pristiphora and differentiates the genus Nematus from Pristiphora on the basis of head morphology.

Adults of the species are somewhat larger than the common housefly, and are superficially distinguishable from other Tenthredinidae by the presence of a transverse red band across the abdomen of both male and female. Males occur in the proportion of 1 to 25 females, according to Marlatt (1929), and they constituted less than 1 percent of the total reared out by Lejeune (1948). The sawfly reproduces parthenogenetically at least in part (Marlatt, 1929). Miles (1936), on the other hand, indicates that only females are found in England. In rearing carried out during the course of the investigations to be reported here, Lejeune's figure of 1 percent males would seem applicable. Mating was never observed in the numerous instances where males were caged with females during the work reported here, and in all observed instances, eggs of virgin females gave rise to larvae.

The females lay their eggs in incisions in the new green growth at the tips of the shoots, the number per shoot depending upon shoot length at the time of oviposition (Marlatt, 1929). Marlatt states that females refused to oviposit until the new growth was one-half inch or more in length, even though they died before ovipositing. The number laid increased in proportion to the length of the new growth, up to a maximum of about two inches, after which there appeared to be no further increase. Dissection of adults reared from cocoons collected in Minnesota in 1949-1950 by the writer showed that the number of eggs per female varied from 40 to 90, the mode falling between 65 and 70 per female. Flight period of the adults occurs from June through July in America, and the adults have a life span of from 10 to 14 days (Thielmann, 1938). Polyakov (1928) states that oviposition took place 2 to 4 days after adult emergence, although observations in Minnesota in 1950 indicate that individuals are capable of laying eggs within the first 24 hours. This discrepancy, however, may derive from differences in emergence, some adults requiring more time than others to escape from the cocoon. Under very dry conditions many perfectly formed adults seem incapable of cutting their way through the cocoon, and die before they can emerge.

Eggs of this species are 1.5 mm. long, white, and kidney-shaped. Development was completed in 7 to 8 days in Minnesota in 1950, but may require up to 3 weeks (Thielmann, 1938). Towards the end of their development, the eggs turn yellowish and become swollen, dark eye spots becoming visible at the end of the fourth day in Minnesota in 1950.

First instar larvae are about 2 mm. long, and appear incapable of feeding on needles of old growth. The larvae are gregarious in the early instars, and feeding proceeds both day and night if temperatures are suitable. Depending upon feeding conditions, development is completed in 3 to 4 weeks. First instar larvae are translucent, acquiring a green color as feeding progresses. The succeeding early instars are bright green with sepia-brown to black heads, while in the mature larva the head is black with the body grayish-green dorsally and pale green ventrally.

Upon completion of feeding, the mature larva falls to the ground and begins to spin and cocoon. The cocoon is at first silvery white and remains so under humidities as low as 40 to 50 percent. Under seemingly optimum moisture conditions (90 to 100 percent), the cocoon turns a light brown within 24 hours. Cocooning usually takes place in the first 2 or 3 inches of top soil and only single individuals are found outside the crown circumference (Polyakov, 1928). This author states further that in Canada and European Russia the sawfly completes its life cycle in one year, but in Western Siberia up to 50 percent of the sawflies may remain in their cocoons for a second winter. Graham (1928) found that a small percentage (2 to 4 percent) carried over a second year under certain conditions.

Pupation in Minnesota took place in June for the most part in 1950, and was completed within 8 to 14 days. The peak of adult emergence in Minnesota occurred on or about July 2nd.

With the exception of one report of feeding on hemlock (Insect Life, 1892), feeding is confined to larch (Larix spp.). Hewitt (1912) was unable to induce larvae to feed on Picea, Abies or Pinus. This author further states that Larix europea (Larix decidua Mill.) is the preferred host under natural conditions, with feeding taking place upon L. leptolepis Endl. (Japanese larch) and L. sibirica Ledeb., (Siberian larch), in addition to L. americana Michx. — L. laricina (du Roi) Koch. (tamarack or Eastern larch).

Survey Results

The intensity and limits of the current larch sawfly infestation have been described in an Administrative Report (Butcher, 1950). Included therein are details of the survey technique and procedure. In summary, significant defoliation is confined within an area of some 15,000,000 acres in northern Minnesota at the present time. Using tamarack acreage estimates supplied by the Lake States Forest Experiment Station and the Superior National Forest, survey results reveal that of 434,120 acres of tamarack in the infested zone, 224,521 acres sustained defoliation in excess of 50 percent; 166,083 acres up to 15 percent and 43,516 acres less than one percent in 1950. The trend from 1949 through 1950 appeared in general to be one of equilibrium. Most surprising, however, was the continued escape from heavy attack which was apparent in stands south of the Iron Range in northern Minnesota. The survey results indicate that with the exception of a recession of defoliation severity on the Chippewa National Forest, the levels of attack were roughly similar in 1950 to those obtained in 1949.

SAMPLING STUDIES

Frass Sampling

Insect excrement, or frass, collection and interpretation as a manifestation of population size and as a record of seasonal development is not without ample precedent (Schwerdtfeger, 1931; Gosswald, 1934; Morris, 1942, 1949). This technique has perhaps a more general application in forest insect studies than in most other phases of entomological work. The chief reason for this, of course, is the inaccessibility of feeding larvae, particularly when dealing with trees of pole size and larger. Visual counts of larvae, sweep samplings and other techniques of the entomologist require drastic modification when applied to this type of work.

The reliability of frass sampling results as a criterion of population size was merely a corollary of the main objective, which was to obtain information on seasonal development of the sawfly. The results, however, have been explored for validity and for possible development of the technique as a satisfactory survey instrument.

Collections of frass were made on 4' x 2' flat cloth trays nailed at each corner to stakes driven into the ground. In this manner the tray was suspended approximately 1 foot from the forest floor. In order to minimize loss of frass from the trays by air currents, a weight was placed in the center of each tray. Thus, while still suspended above the ground, the frass tended to accumulate in the center of the tray. The weight itself prevented flapping of the fabric and minimized loss of frass falling into the tray.

Five stands of tamarack in the vicinity of Cass Lake were selected as permanent sampling stations, because of their diverse history with respect to sawfly attack in preceding years. Three 4' x 2' trays were installed in each stand, with each tray set to catch frass from two trees so that the entire effective tray surface was under foliage. This was accomplished by facing the ends of the tray into the boles of two representative trees. Since all of the stands are so stocked that spacing varies from 2 to 8 feet, it was not difficult to abut the two ends of any tray against two representative trees and still retain all the effective collecting surface in the most advantageous position with respect to foliage. The number of trays used in each area was a compromise with necessity, this being the maximum number that could be handled considering that 60 miles of travel was involved in order to service them. Collections were made every 48 hours beginning with the date the first feeding was observed. Each collection was transferred to metal collecting tins, returned to the laboratory and oven-dried for 24 hours. When this was done the frass was transferred to labeled coin envelopes, and sealed. When all the collections were in at the termination of feeding, each 48-hour collection from each area was screened through 20, 40 and 80 mesh soil sieves. The respective fractions were then weighed and expressed as milligrams of each per 48-hour period. For purposes of evaluating the technique as a reliable method of sampling, only the seasonal totals are used here. These include the sums of all three fractions for the duration of the feeding period. Table 1

shows the comparison of collections from the five study areas, identified in descending order of infestation as South Cass, Portage, Beltrami-Cass Lake and Bena Study Plots. Beltrami and Cass Lake were actually two separate study plots, but are lumped here because they are of the same infestation magnitude, and because the collections from only two trays could be used at Cass Lake.

Table 1. Summarized Seasonal Frass Collections in Four Study Plots Showing Numbers of 4' x 2' Trays Necessary for 10.0 Percent Level of Accuracy

Plot	No. Trays	Milligrams of Frass Collected				Coefficient of Variation	No. Trays Required to Reduce SE . X to 10 percent
		Quantity for Season	Mean per Tray	Standard Deviation	Standard Error		
S. Cass		562,129	187,377	19,175	11,071	10.2	4.2
Portage		190,283	63,427	8,765	5,061	13.8	7.6
Beltrami-Cass		140,897	28,179	5,036	2,248	17.8	12.7
Bena		21,656	7,219	2,427	1,400	33.6	45.2

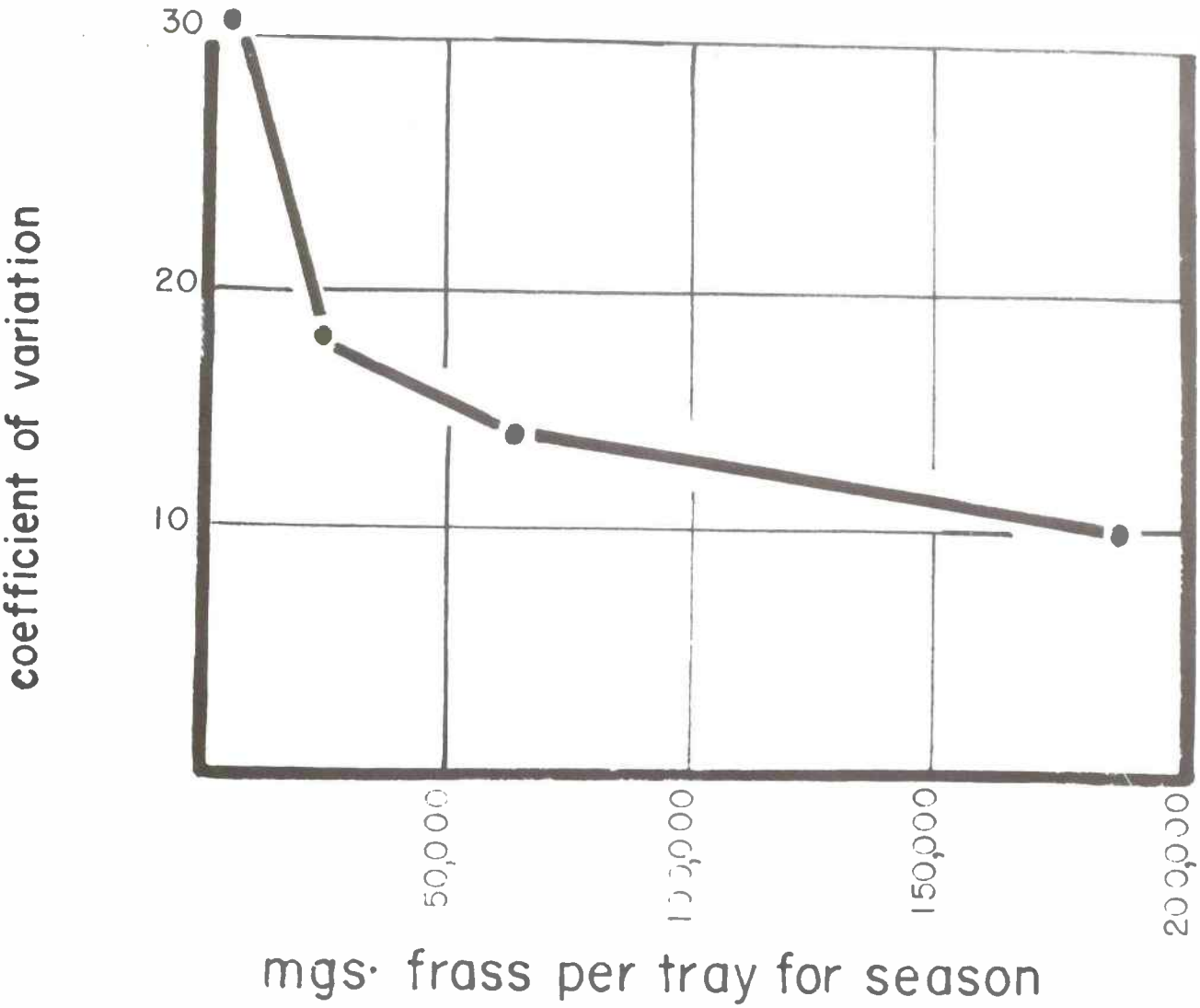
It becomes clear from a study of the foregoing table that 4 orders of infestation magnitude are represented. It also becomes clear immediately that all 4 infestation levels are not sampled with equal accuracy using the arbitrary number of trays employed here. The higher infestations show the least variability between replications, with the level of accuracy decreasing with reduction of population size. Figure 1 shows total frass per season for the 4 groups plotted against coefficient of variation. The severity of defoliation ranged from approximately 5 percent at Bena to 100 percent at S. Cass in 1950. The important thing here would seem to be that at defoliation levels of approximately 15 percent (Beltrami-Cass) and upwards to 100 percent, it would be feasible to install enough trays to get a fairly accurate picture of the infestation. Only at the 5 percent or less defoliation level (Bena) would the number of trays required be prohibitive. Manipulation of the individual sampling unit further, e.g.smaller, more numerous trays using better randomization, is one way in which this error might be reduced, if it were not for the fact that this would increase handling and servicing time even more. It would seem better to use the larger trays at 12 to 14 per plot as the data indicate, rather than to use more and smaller receptacles which would require just as much attention per unit.

Similar work reported by Morris (1949) on the European spruce sawfly with generally lower populations indicates no such loss of accuracy showing up at the lower population densities. Here fifty 2' x 2' trays were used which were distributed at random within the vertical crown projection. With this kind of coverage each tray collected frass from roughly 7.9 percent of the crown projection area as contrasted to a calculated 40.8 percent equivalent area in the case of the larch sawfly work where larger trays (4' x 2') were used.

It is certainly not valid to make comparisons between this work and that done by Morris, who set out to measure the accuracy of his sampling techniques. It does seem likely, however, that at the lower population densities, unless the maximum numbers of sampling units needed were actually employed, the accuracy would be diminished. Apparently the numbers of sampling units used by Morris were sufficient to overcome this tendency since his results fell within limits of 11 percent average of the true population mean, contrasted to 14.8 percent average for the first three larch sawfly plots and 36.8 percent for the last.

From the standpoint of technique, the procedures used in Morris' work and in the larch sawfly sampling differed in several important respects. It was found that European spruce sawfly frass suffered losses in dry weight up to 3 percent through leaching after exposure to dew, and up to 25 percent after exposure to heavy rainfall (duration of exposure not stated in either case (Morris, 1949)). The volume, however, was not affected, nor was it affected by air drying for 5 days or more. Morris converted cubic centimeters of frass, using a glass graduate, into grams by means of a factor: 3.82 cc. equalling 1 gm. A possible source of error, acknowledged by the author but not measured, would be the differential volume occupied by first instar and fifth instar fecal

Figure 1. Frass volume in relation to sample variation.



pellets, and the consequent differences in weight per unit volume of each. Length of the various pellets by instar follows (after Morris):

Instar	Length
V	1.8
IV	1.3
III	1.0
II	0.8
I	0.6

In the larch sawfly work, quantity of frass was determined exclusively through actual weighing. During the course of feeding, collections were made every 48 hours as contrasted to Morris' weekly collections; and rainfall during the feeding period in 1950 was infrequent to the point of being a negligible factor in seasonal frass weight reduction. From the standpoint of frass loss from collecting trays, it appears that Morris' method was superior, since his trays had a greater depth than did those used for the larch sawfly. Here again, however, frass collected only once a week would have to be better protected. Such trays, of course, possess obvious advantages over the shallow receptacles employed in this work, but cost of construction and the additional handling difficulties mitigated against their use.

Conversion of Frass Produced to Foliage Consumed

An understanding of how much foliage a resident population is capable of consuming (i. e., its defoliation potential) must be based on the quantity of foliage consumed by individual larvae. That there should be a correlation between volume of foliage consumed and frass production seems obvious. Taranukha (1937) demonstrated a high correlation of frass dry weight with green weight of foliage before and after feeding (with check experiments designed to measure natural weight loss of foliage during the feeding period) for Porthetria dispar L. Hodson (1941), while not attempting to correlate foliage consumed with frass production, did work out foliage consumption per instar using planimeter measurements of poplar leaves before and after feeding, and expressed frass production per instar in terms of numbers of pellets and their dry weight in milligrams. Others, including Gernitz (1933) and Monro (1935), demonstrated by means of the copremeter the coincidence of various rates of feeding and frass production for Bupalus piniarius L., and Diprion simile Htg. respectively. Morris (1950), concurring in the conclusions of Lebedev and Savenkov (1932), and Taranukha (1937), that studies of food consumption should be based on needle weight rather than on needle counts, calculated green weight foliage consumption for the European spruce sawfly at 0.95 grams per larva as contrasted to 25 grams by Dendrolimus pini L. (Lebedev and Savenkov, 1932). Further, Taranukha (1937) computed coefficients of food assimilation, or Q Values, which are described as weights of food consumed divided by the weights of frass ejected.

It was felt that similar investigations on foliage consumption by the larch sawfly could be carried out with profit, the chief objective being to provide an estimate of foliage consumed based on frass collections in the field. All this work was carried out under insectary conditions so that feeding was practically continuous. The procedure decided upon was to confine 10 newly moulted larvae of each instar to a Petri dish, and immediately introduce foliage from freshly cut tamarack in the form of entire fascicles of known numbers and lengths of needles. This latter was accomplished by cutting all needles to 3 centimeter length and then counting those in each fascicle. In this manner, the numerous replications could be serviced with fresh needles without difficulty, so that an attendant assigned to this work was able to keep the larvae supplied with fresh food, and could prevent accumulation and drying of needles. By way of minimizing high humidity within the covered dishes, the lids were left ajar periodically. Despite this precaution, humidity was excessive in some cases, as is attested by the fungus growth which accumulated on frass in some of the dishes. When this occurred, it became necessary to correct for frass dry weight decline, up to as much as 14 percent. Growth of the larvae was apparently not seriously affected, however, with the possible exception of the early instars, where considerable difficulty was encountered. The feeling persists, nevertheless, that, since this insect is highly gregarious in the early instars, much of the failure was due to attempts to rear the first to third instars in small aggregations. Following is a tabular summary of feeding experiments (Table 2):

Table 2. Food Consumption and Frass Production by Instar

Instar	Replications	Total Number of Larvae Used	Per Individual Larva: Needles Consumed (Mgs.) (Cms.)	(Cms. x .552)	Frass Produced (Mgs.)	Ratio of Frass to Needles Consumed 1/: Cms. Needles/Mgs. Frass (Cms.)	Mgs. Needles/Mgs. Frass (Mgs.)
II	1	10	1.8	0.99	0.8	2.25	1.23
III	2	20	8.6	4.74	3.6	2.39	1.32
IV	4	40	55.1	30.42	23.4	2.35	1.30
V	8	80	319.9	176.56	150.1	2.13	1.18
		Totals	385.4	212.71	177.9		
		Average	-	-	-	2.28	1.26 **

* .552 equals average dry weight in mgs. of 1 cm. of larch needles based on samples from 3 areas.

** Weighted average = 1.2 mg. of needles to 1 mg. of frass produced.

1/ Dry weight

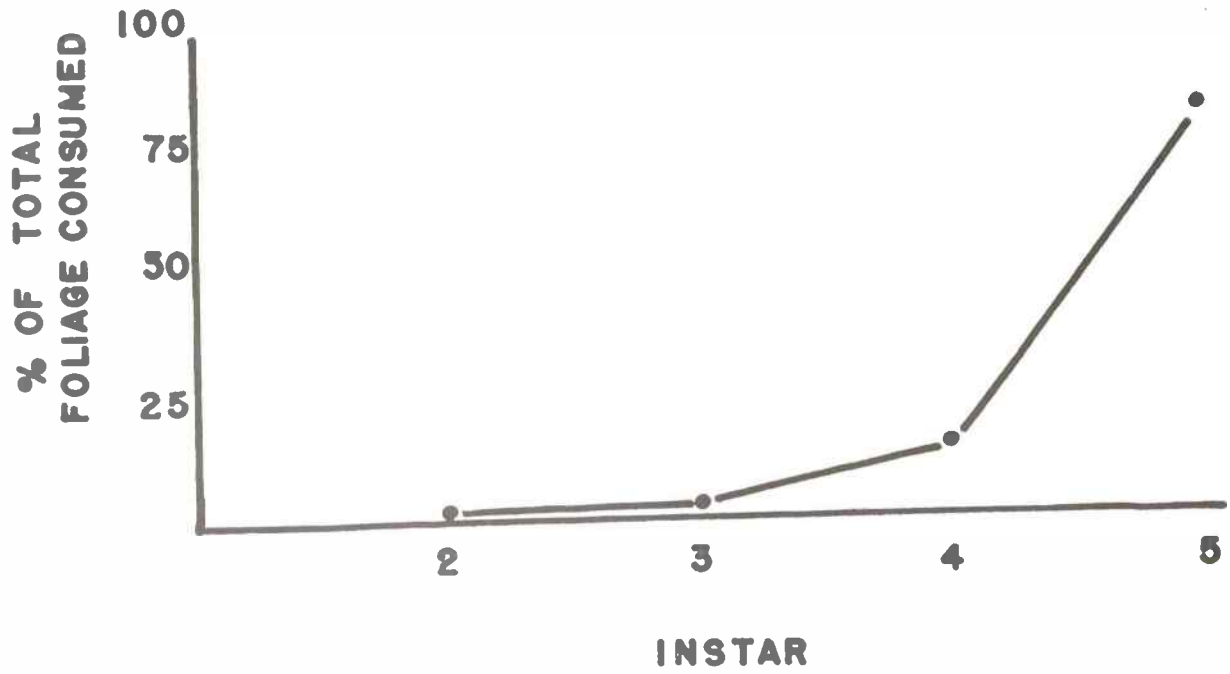
No figures are included for the first instar. Because of the manner in which these rearings were made, if the entire series of ten larvae did not develop to the succeeding instar the series was rejected. It was not possible to rear a series of first instar larvae through to the second in the manner described, and material was not available for additional attempts by the time the technique was abandoned.

While the data given in the foregoing table are valuable as a basis for interpreting frass production per tray in the various study areas in 1950, they should not be accepted as definitive even for those instars adequately replicated, mainly because this work was carried out under conditions not likely to be encountered in the field. If it is kept in mind that this work should be repeated before too much significance is attached to the results, the results themselves provide a very provocative study. For example, in all 4 instars, centimeters of needles consumed bears a relationship to milligrams of frass (dry weight) produced averaging 2.28 centimeters to 1 milligram of frass. Variation was relatively slight in these rearings. By multiplying centimeters of needles by factor (.552), which is the average dry weight of 1 centimeter of uninjured needle length, this figure can be converted to milligrams. Here the relationship averages (weighted) 1.2 milligrams dry weight of needles to 1 milligram of frass produced. If, as seems likely, these ratios stand up under additional replications, it becomes a simple matter to interpret frass in terms of foliage by multiplying dry weight of frass (in milligrams) by the appropriate factor.

A particular derivation of such data as this which always impresses workers who have carried out such feeding analyses is the striking fact that virtually all the foliage is consumed by the last two feeding instars, e.g. 92.9 percent for the European spruce sawfly (Morris, 1949) and 95.5 percent for the forest tent caterpillar (Hodson, 1941). The figure for the larch sawfly is 97.3 percent (slightly higher than it would be if first instar feeding were included). In any case, the first instar total would probably be less than 1 percent of the corrected total. This is more striking when viewed in the following graphic presentation (Figure 2) where percent of the total foliage consumed per instar is plotted.

Projection of frass volume data to the point where it can be used as a criterion of foliage consumption and can form a basis for defoliation estimates is compromised by several factors. That a correlation between food consumption and frass production can be established has been demonstrated. The Q Value (green weight of food consumed divided by the weight of frass ejected) for Porthetria dispar decreased from 7.25 for the first instar to 3.32 for the sixth (Paramukha, 1937). Data presented by Monro for Diprion simile (unpublished thesis, McGill University, reported by Morris, 1949) shows a much smaller variation of Q from 3.5 to 2.5, averaging about 3. Similarly, for Dendrolimus pini (Iebedev and Savenkov, 1932) Q is 3.1 for the entire feeding period. For Pristiphora erichsonii the overall Q value is approximately 2.6, and variation appears small between the last 4 instars.

Figure 2. Foliage consumption by instars.



To assume that the figure is a completely accurate coefficient of consumption to be interpreted literally is naive at best. Variations in size and weight of needles from different twigs on the same tree can be considerable, according to Morris (1949). This worker described variations in weight of spruce needles of from 1 to over 5 milligrams per needle (oven dry weight). Potts (1938) reported that needles from the upper part of the crown of conifers examined were longer than those from the lower. Obviously, these differences in weight and length will influence the quantity of foliage necessary for completion of larval development. In the case of tamarack needles, the variation within a tree previously undefoliated by the sawfly is shown by the data in Table 3.

In order to arrive at an average value for needle dry weight in terms of milligrams per centimeter of needle length for use in the feeding experiments already described, similar data to the above were obtained for trees from three stands in the Cass Lake area. Dry weight in milligrams per centimeter was calculated in all three cases and this figure was used in determining milligrams of foliage consumed per larva (Table 2). A better control over the experiment would have resulted if all needles for feeding had been taken from the same stand, but then in actual practice a stand factor would have been needed to correct for stand differences. The size of the variation in needle dry weight per centimeter encountered in the course of concomitant foliage analysis studies was not anticipated until the feeding work was well along. It is felt that since the method of selection of foliage for feeding was of a random nature, the average factor of the three stands at the various crown levels best expresses the length/weight ratio of the foliage used in the experiments.

Generally speaking, it is not entirely valid to assume that a given volume of frass represents a given number of needles. Many insects feed wastefully; e. g. Taramukha (1937) had to increase his figures of foliage consumption for Porthetria dispar by 30 percent to obtain actual weights of foliage destroyed. Additional factors, such as drying of needles on severely defoliated twigs would result in greater damage to the tree than might be expected, so that estimates of numbers of larvae necessary to defoliate a tree completely might be in error as much as 75 percent (Schwerdtfeger, 1930). The larch sawfly, however, with the exception of the first and second instar, in consequence of its gregarious feeding tendencies consumes entire needles as a rule. The first instar larvae chew only small notches out of needles from current year's growth, but subsequent stages consume the entire needle down to the base of the fascicle. The effect is generally to strip the branch completely, leaving only the relatively short needles on elongating shoots.

Table 3. Relation of Position in Crown to Needle Size, Weight, and Weight per Unit of Volume for 1950 Tamarack Foliage [1]

Third of Crown	Year's Growth from which Fascicles Taken	Total Length of Needles (M.)	Total Weight		Weight per Unit of Volume [2]	
			Green (Mgs.)	Dry (Mgs.)	Green (Mgs.)	Dry (Mgs.)
Top	1949	7.64	800	383	1.05	0.50
	1948	8.74	935	439	1.07	0.50
	1947	6.48	630	301	0.97	0.46
	1946	7.04	655	319	0.93	0.45
	Average	7.48	755	361	1.00	0.48
Middle	1949	5.59	610	283	1.09	0.51
	1948	6.04	620	282	1.03	0.47
	1947	6.31	620	283	0.98	0.45
	1946	7.16	780	338	1.06	0.47
	Average	6.28	658	297	1.04	0.47
Bottom	1949	4.20	345	180	0.82	0.43
	1948	5.91	443	225	0.75	0.38
	1947	3.90	357	164	0.91	0.42
	1946	6.10	501	242	0.82	0.40
	Average	5.03	412	203	0.83	0.41

1/ Values given are for a total of 10 fascicles in each case.

2/ Figures are milligrams per centimeter.

In order to implement the results of rearing research just discussed, some measure of the foliage present in a given stand was in order. The preceding discussion has illustrated the difficulties likely to be encountered, but the works of Potts (1938), Gäbler (1940) and Hodson (1941) demonstrate the validity of the approach. Since a measure of the foliage requirements of individual larvae is available and can be expressed in terms of needle dry weight, it seemed most logical to determine total foliage per tree in the same manner. Trees from three study plots, the history of which were known with respect to previous defoliation by the sawfly, were selected for sampling. Trees in these stands were approximately even-aged and the various stands were approximately the same age (30 to 35 years). Stocking differed somewhat, ranging from 800 to 900 stems per acre. The method used to estimate foliage was to determine average trees for each stand on the basis of measurements made of ten trees selected at random. Crown length, crown diameter and DBH were the characteristics upon which greatest emphasis was placed. When the average of these characteristics was arrived at, a single tree most fitting these figures was selected for cutting. The trees were felled in such a manner as to cause minimum loss of foliage. When this was done, the limbs were removed close to the stem, and further dismembered so that the entire foliage bearing portions of the tree could be placed in large cardboard cartons. The containers were then transported to storage in the insectary until all of the needles had dropped. When all needles had fallen, they were transferred to a large paper bag, left open, and oven dried at approximately 110° F. for 3 to 4 days. Subsequently, small twigs and other foreign material were removed and the contents weighed. This provided a measure of dry weight of the foliage present on average trees in each stand to which the defoliation potentialities of a given insect population could be related. Admittedly, more replications are necessary in order to measure the total foliage accurately, but pressure of other work prevented elaboration on this phase in 1950.

By means of the conversion factor already referred to, it is possible to express the dry weight of foliage in terms of centimeters of needles. This factor was determined for the three areas sampled in the manner described in discussion of Table 2. It need only be mentioned here that the figure was variable and generally lower in the stands with the lowest incidence of defoliation in previous years. This will be discussed in more detail in a later section.

The following Table 4 gives a breakdown of total foliage on representative trees from each of the Beltrami, Cass and Bena plots, expressed in milligrams dry weight per tree. The second column shows the total frass collected in each of five areas in 1950 (average dry weight in milligrams for an 8 square foot collecting surface). Column 3 converts frass dry weight to foliage using the coefficient 1.2 which is the ratio of milligrams dry weight of needles consumed to milligrams dry weight of frass ejected. Column 4 shows the calculated foliage consumption per tree in the various areas. Here the quotient obtained from dividing total perpendicular crown projection area by the 8 square foot sampling unit is multiplied by the volume of foliage consumed in a vertical crown projection area of 8 square feet (Column 3).

Table 4. Breakdown of Frass Collected Showing Calculated and Observed Defoliation

Area	Dry Weight of Total Foliage on Sample Tree (Mgs.)	Per 8 Sq. Ft. Tray: Total Dry Weight of Frass Collected (Mgs.)	Per 8 Sq. Ft. Tray: Calculated Total Dry Weight of Foliage Consumed 1/ (Mgs.)	Calculated Total Dry Weight of Foliage Consumed per Tree 2/ (Mgs.)	Defoliation: Calc. (Percent)	Defoliation: Obs. (Percent)	Expected No. of Cocoons per sq. ft. 3/
Beltrami	785,032	28,543	34,251	90,765	11.6	10.0	20.1
Cass	567,530	27,634	33,160	81,242	14.3	15.0	19.4
Bena	1,284,712	7,219	8,663	21,224	1.7	5.0	5.1
S. Cass		187,377	224,852	550,887	-	100.0	131.6
L. Portage		63,112	76,094	186,430	-	20.0	44.8

*Note: Foliage removed by sawfly defoliation prior to cutting trees was calculated on the basis of frass production to date of cutting. The corrected totals are shown in this column. Since defoliation was comparatively light in all areas in which foliage samples were taken, this calculation does not contribute greatly to the error involved in the total.

1/ Calculated total dry weight of foliage consumed per tray = frass per tray x 1.2.

2/ Calculated total dry weight of foliage consumed per tree = $\frac{\text{sq. ft. crown closure}}{8} \times$ Foliage consumed per tray.

3/ Expected number of cocoons per square foot = $\frac{\text{total frass per square foot.}}{177.9}$

By dividing this last figure by total dry weight of foliage on the sample tree (for the first three plots only), an estimate of defoliation in each area is possible. This can be compared to the visual estimates labeled "Observed percent defoliation." Further, by dividing the total weight of frass produced by all instars of individual larvae into the seasonal frass accumulation per square foot, a figure on approximate numbers of cocoons per square foot can be arrived at.

Obviously, these figures are not to be accepted at their face value. Sources of error are numerous. For example, (1) although the value derived for total foliage on the sample trees can be considered fairly accurate, and the trees themselves average with respect to foliage for their particular stands, there are no replications. In a further development of this phase of the study at least a dozen trees should be used for each stand and variation computed. (2) Determinations of total frass are considered reasonably accurate - at least they fall within 14 percent of the true mean in the case of four of the stands, but there is ample room for improvement as was discussed in the foregoing section on this technique. (3) The calculated values for the weight of foliage consumed (Table 4) are based on the assumption that the coefficient 1.2 accurately represents the ratio of foliage dry weight to dry weight of frass. Despite the fact that this is a weighted average, the feeding experiments upon which this figure is based were carried out under only one set of conditions and although there were replications under these conditions the research was not repeated. Finally, estimated numbers of cocoons per square foot derived by these calculations must be based on the assumption that accumulative frass weight was directly convertible to larval numbers per se. This could not be so, since population reduction in the larval stage must always take place. Natural mortality due to dislodgement of individuals by wind and rain and premature drop because of an exhausted food supply, to mention a few, would compromise the accuracy of this figure indeterminately.

When all these and many other shortcomings of these data are acknowledged, the fact remains that such a basic approach to population analysis may prove to be of inestimable value, both to the ecologist and to the practical field worker. Properly refined, it can form the basis for research and interpretation of natural mortality, for example, since the difference between the size of the cocoon population and the expected cocoon population will be a measure of the toll taken by biological and meteorological factors prior to cocooning. From the sampling standpoint any light shed on the parameter gives meaning to its statistics, and whatever the shortcomings of these data, they nevertheless bring the parameter closer to definition.

One of the principal by-products of this work which is more obvious than the data so far presented indicate, is the apparent effect of defoliation on subsequent foliage volume. The history of sawfly attack on each of the three plots for which sample trees were cut and total foliage determined is quite different. More detailed data on this will be presented later, but for the moment suffice it to say that oviposition injury in previous years suggests that the Cass plot sustained defoliation of 50 percent or over for the three years 1947-1949; Beltrami sustained heavy defoliation (50 percent and over)

in 1949 with moderate attack (20 - 49 percent) in 1948, and light injury (5 - 19 percent) in 1947. Bena was not seriously attacked in many of these years, very light injury (0 - 5 percent) taking place in 1947 - 48 and light injury occurring in 1949. The fact that 1950 foliage volume at Bena is 2.3 times that of Cass and 1.6 times that of Beltrami (as determined from the restricted sample) could not be taken seriously if other manifestations of decadence were not in agreement with this pattern. The collective evidence strongly suggests that a large part of these differences in volume, since they correlate with injury in the past, are due to the effects of previous sawfly defoliation. If this is true, then a cocoon population of 19.5 per square foot at Cass might constitute 2.3 times as much of a menace in this stand as it would at Bena, since the latter would seem to possess 2.3 times as much foliage. Judgment on the tenability of this premise should be reserved until a subsequent discussion of decadence manifestations other than foliage volume has been examined. This brief reference to the subject is presented prematurely, since its implications are partly concerned with sampling error and the proper interpretation of sampling results in terms of defoliation potential.

NATURAL DETERRENTS TO POPULATION SIZE

A discussion of stand and site factors that influence the course of a sawfly infestation is the subject of this section. Such influences are not always clearly defined and are sometimes difficult if not impossible to express in quantitative terms. For example, a high water level in a particular tamarack stand influences the insect directly insofar as it retards pre-pupal or pupal development or causes actual mortality. This effect can be measured and its consequences properly evaluated. On the other hand, these same high water levels might influence the host species to the extent that seasonal elongation of shoots is deferred and/or restricted. As a result, those sawflies above the water table which develop normally are confronted with short shoots inadequate to support large numbers of eggs per shoot. Observation of, and laboratory failures with small aggregations of first and second instar larvae strongly suggest that there is an inverse relationship of larval mortality to colony size. In addition, even if survival were high, defoliation would not be as great, particularly where small egg groups were the rule and the numbers of larvae hatching might be too small to utilize all the food available.

The foregoing illustrates the complex nature of this problem. Investigations bearing on this subject can be divided roughly into two major categories: (1) effect of tree growth characteristics on population size, and (2) effect of water level on both the tree and the insect. Virtually all the data pertinent to this section were obtained as a by-product of other major lines of research, or from incidental pursuits which were not emphasized.

It will be recalled that the larch sawfly causes injury through oviposition in terminal growth of the current season. In the following discussion, oviposition in the terminal shoots will be referred to as "shoot injury." The approach to this problem presupposes that the insect is actually unable or unwilling to oviposit in old growth or in growth which already contains eggs of another female, i. e. on the opposite side of such shoots. Oviposition experiments demonstrate conclusively that the insect is capable of laying eggs in the woody growth of the previous year and when confined with access to only one shoot already containing eggs of another female will lay in that one also, either above those already laid or on the opposite side of the shoot. Neither of these peculiarities are observed in the field to any significant degree, and until evidence is on hand that females will lay in such shoots if free to move about in search of new growth uninjured by oviposition, it is assumed that the phenomena are not common.

Effect of Tree Growth Characteristics on Population Size

Lejeune and Wong (1949) cite drastic decline in size and number of new shoots suitable for oviposition as a possible deterrent to sawfly population size. The most logical lines of investigation to pursue in evaluating this contingency as a factor in stand resistance would seem to be studies on (1) actual length of previously injured shoots the year following injury, (2) length of uninjured shoots on trees previously heavily defoliated as compared with average lengths from stands previously undefoliated or relatively so, (3) seasonal development of the same shoots and their relative length at the time of maximum adult abundance. To measure a 1950 terminal after the growing season has been completed gives little information on the available length at the time of adult activity.

The following Table 5 shows the corresponding lengths of injured and uninjured shoots from the top third of crowns in four areas, and the date at which the measurements were made. This gives some idea of the relative lengths of the two on a seasonal basis, and since injured and uninjured lengths for each stand on a given date are from the same primary branch; the figures are comparable and the averages for the season should be comparable also.

Table 5. Comparison of 1950 Growth Lengths of Shoots Injured and Uninjured in 1949

Area	1950 Shoots Injured in 1949		1950 Shoots Uninjured in 1949		Date
	Number of Measurements	Average Length (Cms.)	Number of Measurements	Average Length (Cms.)	
Bena	10	4.5	4	5.1	6-21
	10	5.1	10	15.4	7- 3
Portage	3	1.6	10	2.0	6-22
	10	1.8	10	2.5	7- 5
	10	3.3	10	4.8	7-11
	10	3.1	10	5.3	7-20
Beltrami	10	3.6	10	3.6	6-22
	10	2.0	10	2.2	7- 5
	10	2.7	10	4.0	7-12
	3	4.2	10	6.4	7-19
	4	10.2	10	10.7	8-10
S. Cass	10	3.4	10	8.5	6-25
	5	2.4	10	3.8	7- 5
	2	4.6	10	5.2	7-12
	3	4.4	10	7.3	7-19
Total	110	—	144	—	
Average	—	3.8	—	5.8	

From these figures it appears that the direct effect of previous injury on individual shoots was to retard their development by about 35 percent. This conclusion is misleading, however, since the effect is apparently not the same in stands having sustained different degrees of injury in the past. The data in Table 6 tend to illustrate this point. Here 1949 growth of terminals injured and uninjured in 1948 is compared for two areas - South Cass, moderately defoliated in 1948 (20 - 49 percent) and very lightly defoliated in 1947 (0 - 5 percent); and Cass, heavily defoliated in 1947-48 (50 percent plus).

Table 6. Effect of Previous Injury on Shoot Length

Area	1949 Shoots Injured in 1948		1949 Shoots Uninjured in 1948	
	Number of Measurements	Average Length (Cms.)	Number of Measurements	Average Length (Cms.)
S. Cass	8	7.7	10	25.4
	5	3.3	10	11.7
	1	4.8	10	14.2
Total	14	—	30	—
Average	—	5.3	—	17.1
Cass	4	2.8	4	3.8
	4	3.7	4	3.6
	4	2.4	4	2.8
	4	3.7	4	3.5
	4	2.4	4	5.3
Total	20	—	20	—
Average	—	3.0	—	3.8

The difference in uninjured and injured shoots between the two areas cannot be considered significant on the basis of the limited data obtained. There is little reason to doubt that such a relationship of injury to subsequent shoot growth does exist, however, and it might be summed up in the following manner. Light attacks by the sawfly on previously undefoliated or lightly defoliated trees will result the following year in markedly reduced growth on those shoots injured by oviposition. These differences may well be of the magnitude suggested by figures for S. Cass where the difference is 69 percent between shoots on the same primary branch. Trees heavily defoliated for two years previously show a length differential the following year of smaller magnitude (21 percent for Cass), but the overall shoot length is drastically reduced. Elaboration on this phase properly belongs in the succeeding section entitled Manifestations of Tree Decadence. It is mentioned here merely to point out that the shoot injured by oviposition in itself is probably not directly a serious deterrent to succeeding years' populations because even at high population levels there still would be plenty of previously uninjured shoots. Evidence for this is offered by data on all plots relative to percentage of shoots attacked. Table 7 shows percent of 1949 shoots injured by oviposition and the defoliation for that same year.

Table 7. Percent of Available Shoots Injured in 1949

Area	Total Shoots 1949	Injured 1949	Percent Injured 1949	Percent Defoliation 1949
Case	607	299	49.3	75
Beltrami	916	327	35.7	100
Portage	1,402	137	9.8	80
S. Cass	1,263	94	7.4	70
Bena	1,336	32	2.4	5

The total number of shoots for 1949 was obtained by actual count of new shoots on three primary branches from the top, middle and bottom thirds of the crowns of 5 trees from each of the 5 study plots. Although there were plenty of unoccupied shoots suitable for oviposition, trees from each of the 5 stands showed a decrease in average uninjured shoot length (on the top third of the crown) in almost direct proportion to percent of shoots injured. For example, interpreting 1949 shoot injury as reflecting relative defoliation intensity in 1948, there is a good correlation between percent of shoots injured in that year (1948) and their length in centimeters in 1949.

There is no reason to seriously question the importance of previous injury in deriving this interpretation. For its basis, Figure 3, which shows the relationship of oviposition injury in 1948 (percent of total available shoots) to length in centimeters of uninjured shoots in 1949 in the top third of the crown, should be examined.

The thesis that oviposition limitations are a significant factor in deterring sawfly injury to tamarack thus seems tenable; but not for the reasons so often advanced. Conceivably, a high population carrying over from the preceding year could in effect have laid the groundwork for its own decline by injuring and thus reducing the effective size of the egg laying sites the following year. This may occur, but the effect does not seem to be direct and restricted to the shoot attacked; it is cumulative and is an expression of tree decadence brought on by oviposition and defoliation.

As mentioned earlier, the total annual growth of shoots when measured at the end of the growing season is not an accurate criterion upon which shoot length as a population size deterrent can be based, because oviposition occurs before shoot elongation is complete. Actual counts of eggs per centimeter of shoot length indicate that a female will lay 16 eggs per centimeter (20 shoot sample) on the average. Total annual length of shoots in all the plots studied would give the impression that all the areas have shoots of a size adequate to support substantial colonies, even after sustaining up to 3 years of heavy defoliation. This is demonstrated by the figures for shoot length, based on measurements of uninjured 1948-49 shoots from 3 crown levels in all areas, presented in Table 8.

Figure 3. Relationship of 1948 oviposition injury to 1949 shoot length.

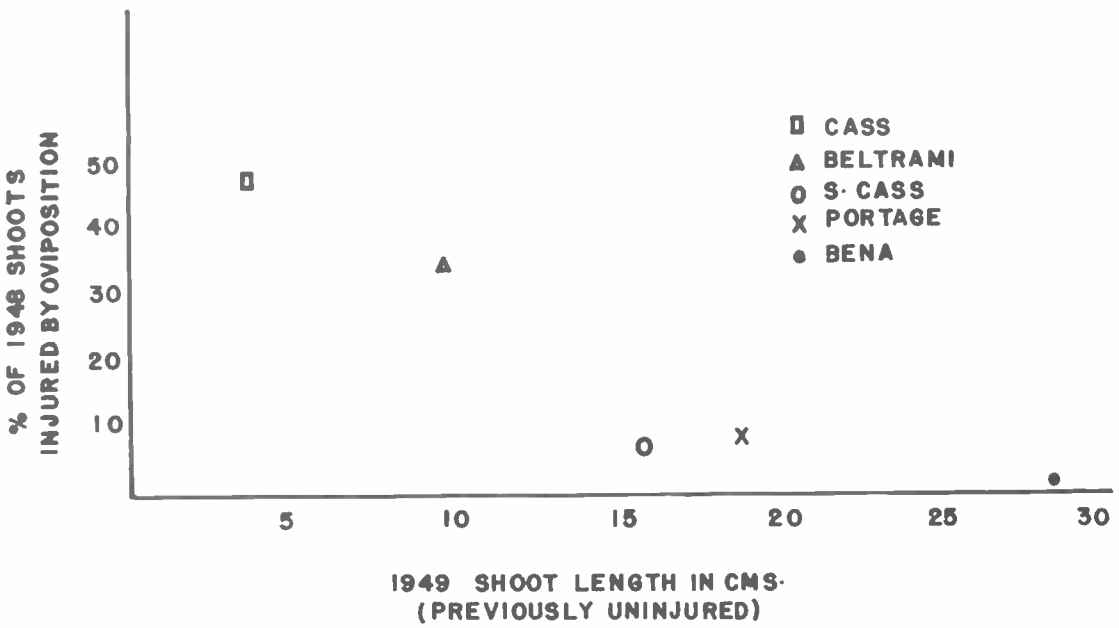


Table 8. Total Annual Shoot Length for Five Study Areas in 1948-49 at Top, Middle and Bottom Thirds of Crown

Area	Length in Cms. 1/ T.	M.	B.	No. Eggs Possible per Shoot 2/ (Cms. x 16) T.	M.	B.	Length in Cms. 1/ T.	M.	B.	No. Eggs Possible per Shoot 2/ (Cms. x 16) T.	M.	B.
Cass	4.0	2.5	2.2	64	40	35	5.6	4.2	2.8	90	67	45
Beltrami	9.5	3.5	3.5	152	56	56	19.0	8.0	3.0	304	128	48
Portage	19.0	7.0	5.0	304	112	80	23.0	9.0	7.0	368	144	112
S. Cass	15.5	5.0	4.2	248	80	67	23.5	9.0	6.4	376	144	102
Dena	28.2	6.2	5.0	451	99	80	28.0	9.0	6.2	448	144	99

T. - top M. - mid-crown B. - bottom crown

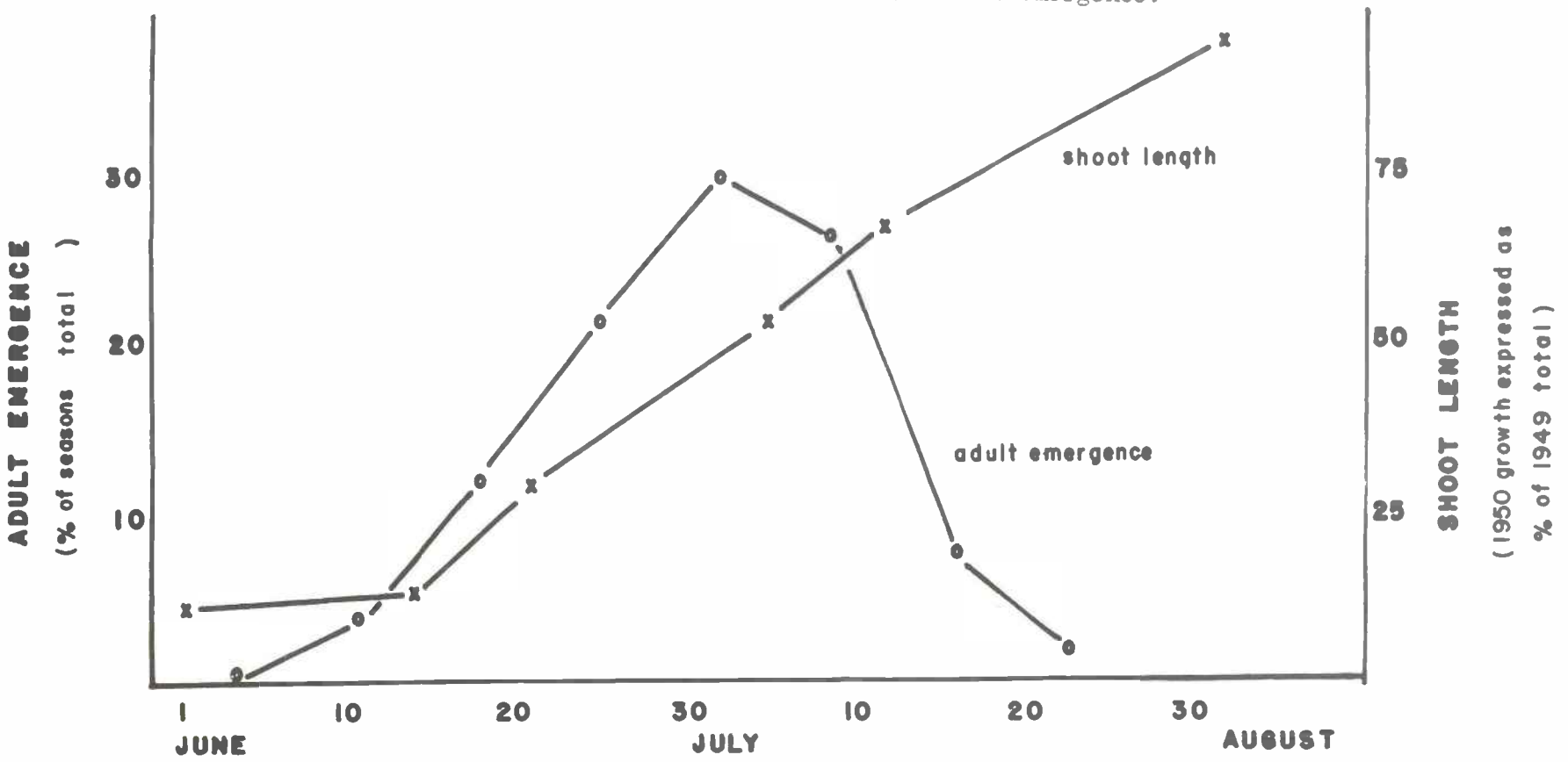
1/ Average of 50 measurements per crown third with the exception of Cass which is average of 25 measurements per crown third.

2/ Centimeters of shoot length x 16 (Average number of eggs per Cm.)

The above data show that on the basis of shoot growth for the entire year, the aggregations of eggs would not be seriously limited in size as a consequence of previous injury. Cass, which shows the most pronounced effect of previous feeding (in terms of shoot length reduction) would seem capable of supporting eggs of one half a colony (30 - 40 eggs) even in the lower crown third. This is entirely erroneous, however, since adult emergence in 1950 would indicate that maximum adult activity takes place at the time shoot elongation is approximately 50 percent completed. In wet areas it would seem that elongation may be retarded still more at the time of greatest oviposition activity. The following graph (Figure 4) shows an adult emergence curve for a dry area obtained from natural emergence of adults in a cage 3' x 3' x 1' countersunk in the ground to a depth of 6 inches. Here percentage emergence of adults is plotted at weekly intervals in conjunction with a terminal elongation curve (shoots from lower crown). Elongation of the shoots is also expressed as percent, but as percent of 1949 total length. Total average length by August 11, 1950 of the 5 shoots upon which this curve is based was 98 percent of the 1949 seasonal total. Measurements were made at the edge of a stand, and although 10 shoots were selected initially, oviposition injury rendered 5 of these useless before the date of the final measurement.

It is conceivable that 70 percent of the adults in this area could have emerged before shoot growth was 50 percent of the 1950 total. Assuming that adult females do live for two weeks, as reported by Thielmann (1938), this would still mean that most of the eggs are laid before shoots have achieved two-thirds of their ultimate growth. Granting an average of 50 percent as the elongation point which corresponds to the high point of oviposition, quite a different picture of suitability of shoots in the different infestation levels obtains. Taking half of the figures in the column designated "Number eggs possible per shoot", (Table 8) a more logical estimate of availability is possible. That this might prove an important factor in survival is apparent, particularly in the Cass and Beltrami stands. It could mean small colonies subject to the already suggested shortcomings of such colonies with respect to survival and defoliation potential. If a colony average of 65 larvae is used, it seems likely that 50 - 60 percent of the emerging females at S. Cass in 1949 would each lay eggs in an average of between 2 - 4 shoots per colony. This means (1) that colonies are smaller (remembering that as averages the figures are representative of many shoots with considerably smaller egg capacities), (2) many more shoots are required, and (3) the difficulties of finding these extra shoots are compounded by the additional competition for the fewer unoccupied sites. With little information available on the searching ability of female sawflies, this reduction in suitable shoots and its effect upon their chances of finding proper oviposition sites can only be speculated upon. The fact is that adult females are very reluctant fliers, but were observed to be capable of strong flight on infrequent occasions. Observational evidence would suggest that most searching is carried out by crawling from one shoot to the other, using a trial and error method on each shoot encountered.

Figure 4. 1950 terminal growth expressed as percent of 1949 total plotted with percent of total 1950 adult emergence.



Oviposition has been achieved under laboratory conditions by females within 24 hours of their emergence, so that ample time would seem available for extensive searching. It seems likely that the physical problem of egg disposal due to curtailed shoot length may be a factor; and that high mortality in the small larval aggregations which are a consequence of shorter shoots also is involved.

Quantity of Foliage as a Limiting Factor

The foregoing discussion relating to intraspecific competition deals mostly with the effect of shoot size. Another and perhaps more important factor in population size restriction derives from the decrease in foliage volume which appears to follow severe defoliation. To state that this is an important limitation, on the basis of foliage volume measurements made in three areas using a single tree sample, would be unscientific at best; but supplementary evidence is available from detailed needle samplings of the crowns of specimen trees in these same areas.

Briefly, there appears to be an important difference in the foliage characteristics of the trees in the Cass plot as contrasted to the Bena plot. As suggested by Potts (1938), the normal condition would be that those needles at the top of the crown would be longer than those at the bottom. Data obtained for specimen trees, one from each of the Cass and Bena areas (former heavily hit in preceding years, the latter negligibly defoliated), are offered for comparison in Table 9. These figures were arrived at by measuring average length of needles. Length in meters is thus the aggregate length of the individual needles in 10 fascicles. Data for Bena have already been presented in Table 3 in detail and can be referred to for further information on the manner in which the samples were selected. The data are averages of 40 fascicles per figure.

Table 9. Relationship of Needle Size to Position on Crown for Heavily Defoliated and Undefoliated Stands

Third of Crown	Area	Length of Needles in 10 Fascicles 1/ (Meters)	Green Weight 10 Fascicles 2/ (Mgs.)	Dry Weight 10 Fascicles 2/ (Mgs.)
Top	Cass	3.42	473	205
	Bena	7.48	755	361
Mid	Cass	4.44	494	242
	Bena	6.28	658	297
Bottom	Cass	4.39	566	268
	Bena	5.03	412	203

1/ Length is summation of lengths of individual needles for 10 fascicles (4 replications).

2/ Based on 4 replications.

Comparisons of measurements from the two areas at least suggest that the total volume of foliage for comparable trees in these stands would be of different magnitudes. The fact that the foliage volume for the Cass Lake specimen tree (defoliated previously) is only 44 percent of that for a comparable tree from the Bena area (negligible defoliation) would further indicate that additional work might throw light on the hitherto inexplicable infestation recessions which follow heavy attacks. As a matter of record, Graham (1931) found the reduction in dry weight per fascicle to be directly correlated with the intensity of previous defoliation; dry weight loss per fascicle decreasing as much as 1/3 on branches known to have been defoliated the previous year. This latter effect points up the possibility that only the tops of the Cass trees may have been severely defoliated previously. This would be a definite possibility, of course, were it not for the indications of heavy infestations evidenced by oviposition. There is no disposition to accept the data offered at its face value, but a skeptic need only to have viewed a stand that had been completely stripped in 1949 and one with no previous history of defoliation to appreciate the striking luxuriance of the latter's foliage compared to that of the former in 1950.

Water Level as a Deterrent to Population Size

The problem of inundation of sawfly cocoons and its effect upon survival has been the subject of speculation and research (Lejeune and Filuk, 1947), whereas the possible implications of shoot retardation in relation to water level has not received similar attention. In the preceding discussion of shoot length as a factor in population reduction, emphasis was placed on the effects of previous defoliation as contributing to this condition. The possibility that high water may also contribute to production of smaller shoots deserves consideration.

The data to be offered in this connection were obtained from routine samplings carried out to further investigations on the effect of immersion on cocoons and mature larvae. Since the amount of cocooning universe inundated was of importance, water levels in the 5 study areas were measured in two ways. The first was to determine the rise and fall of the water level in inches on stakes in permanent wells dug in each stand. The second method was to estimate percent of the vertical crown projection area that was covered by surface water. The first method was relatively simple and accurate. The second was not as readily made and was of course subject to some error. In lieu of constructing elaborate grids using string to divide the surface into easily measured blocks, it was decided that a more useful technique, despite the probability of error, would be visual estimates made by at least two individuals. It was considered desirable to obtain estimates of inundation in all 5 study areas on a weekly basis throughout the field season, so that a more precise method would not have been practical.

At the beginning of this work, 10 trees in each stand were tagged and numbered consecutively. These trees were selected at random and the distance between trees 1 - 10 was approximately 200 feet. Each observer determined the vertical crown projection limits and took his position at a point on the circumference. From this spot the crown projection area was visually divided into two quadrants and estimates of percent of each under water were made. Then, moving to a corresponding position on the opposite side of the tree, the same thing was repeated and the four estimates averaged. Never was the discrepancy between the estimates of two individuals for the 10 trees in any area greater than 5 percent, and in over 90 percent of the cases the estimates were within 2 percent. A check on the accuracy of the method was made with the water rise and fall as measured on the stake in the Little Portage Lake plot. This was the only plot of the 5 that exhibited fluctuations over a wide enough range to make such a comparison possible. Figure 5 shows water level in inches plotted against the percent of the cocooning universe inundated (the respective stake levels were obtained at the same time as the water level estimates). These data yield a highly significant coefficient of correlation suggesting that the estimates are sufficiently accurate to be useful. As the curve indicates, the water table in a bog may fluctuate over a range of nine inches. In a normal year the probability is that in some bogs the degree of cocooning universe inundated may drop below 10 percent by the first week in June, or earlier. Prolongation of flooding due either to heavy spring rains or artificial damming would tend to change this picture.

Because shoot elongation can be interpreted as a measure of seasonal development the data in Figure 6 are presented to show the relationship of high water to shoot retardation. Shown in this figure are crown projection inundation estimates which differ over quite a wide range. The South Cass plot, for example, did not contain surface water exceeding 10 percent of the crown projection area after the first week of June; those of the Beltrami, Bena and L. Portage plots were progressively wetter in that order. The Beltrami picture would seem to represent the normal condition for this stand under the rainfall conditions prevailing in the spring and summer of 1950. The Bena and Little Portage Lake plot water tables remained at a high level because of a road improvement program which occluded the source of drainage, Portage being much more affected than was Bena. The figure shows percentage of crown projection area containing surface water, the level at any particular date is assumed to be that prevailing up to the succeeding estimate, in most cases a week later. Plotted on the same graph is a curve of shoot elongation for 1950 expressed as percent of 1949 total growth of the same shoot. These figures were obtained from measurements of shoots on 10 branches cut at the dates shown. More points would improve this picture quite a bit, and also more tree replications would be desirable, since it cannot be assumed that all of the five trees comprising the record for any one stand were uniform in their growth response.

Figure 5. Percent cocooning universe inundated plotted against rise in water level in well.

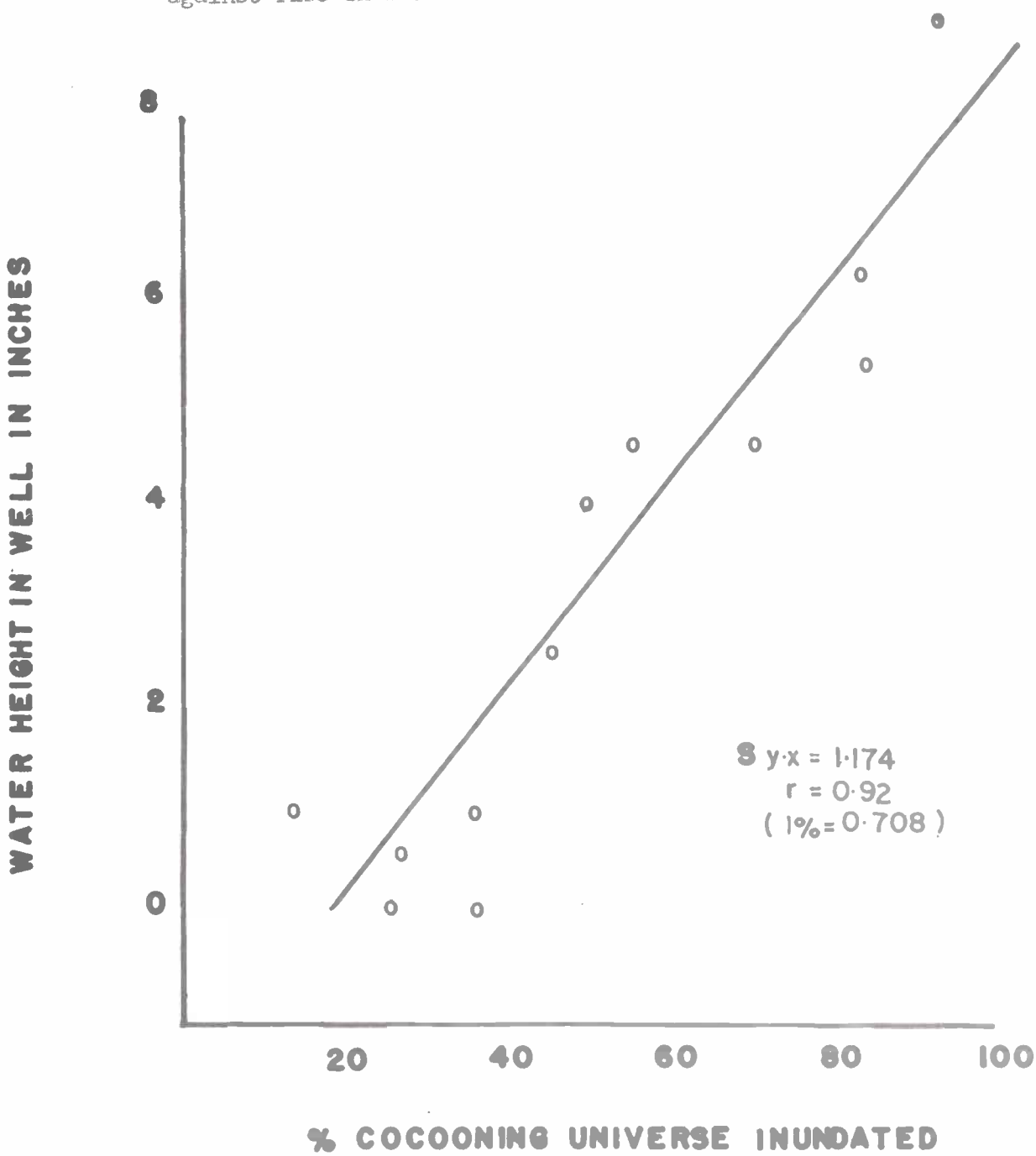
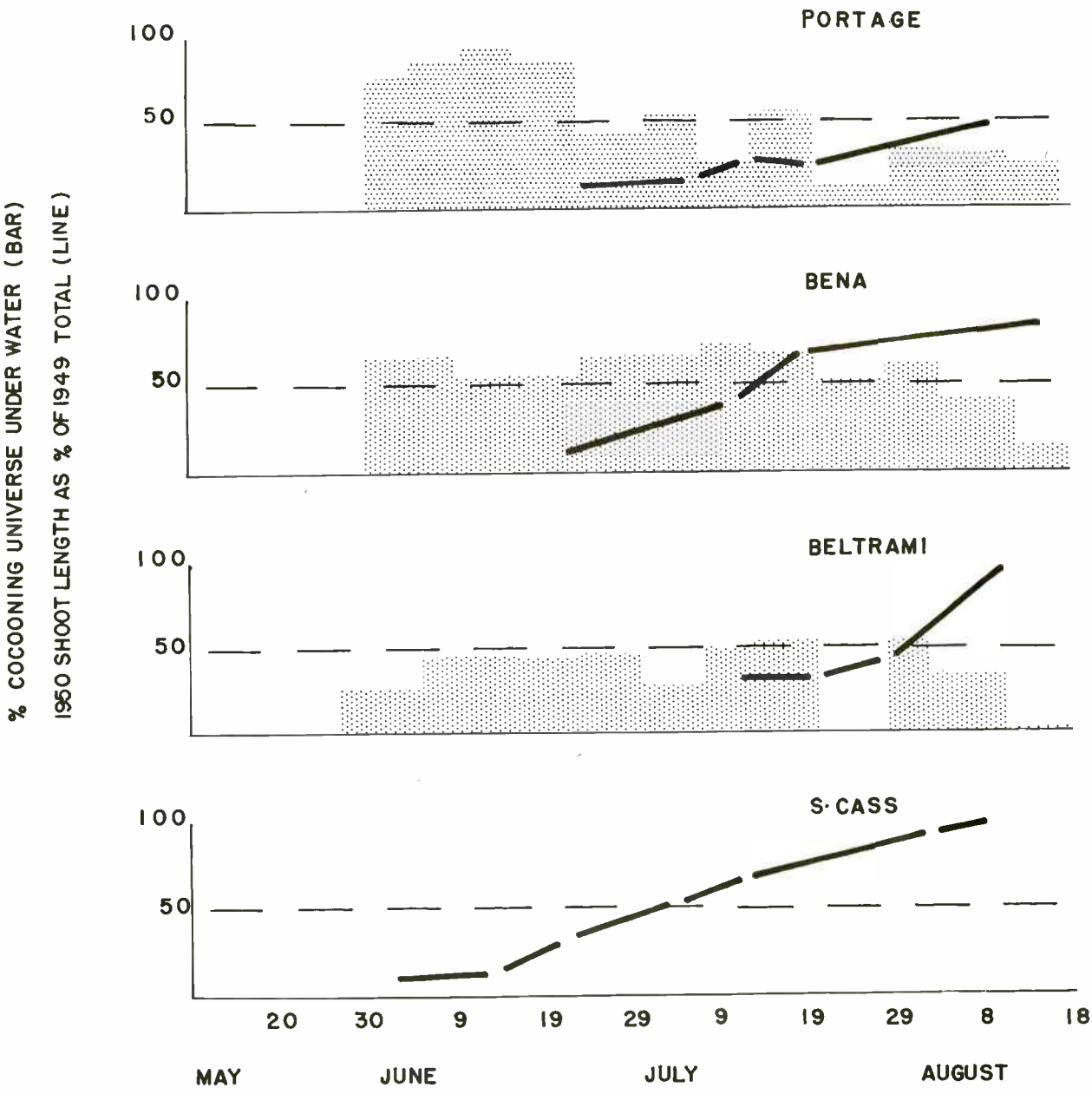


Figure 6. Percent cocooning universe under water in relation to seasonal shoot elongation.



The chief reason for presenting this material is to show that it is a possible factor complicating interpretations of larch sawfly injury as a cause of shoot length retardation. However, its possible role as an influence in curtailing oviposition sites is certainly an important consideration, which can only be suggested by these data. It is impossible, for example, to more than guess at the relative importance of sawfly defoliation and water levels in trying to explain the conditions recorded. The Portage plot, which sustained moderate defoliation in both 1948 and 1949, undoubtedly suffered a growth decline in 1949, and also in 1950 due to defoliation, as will be demonstrated in the succeeding section of this paper. Beltrami was similarly affected in 1948 and 1949, but exhibited a better (if also somewhat retarded) growth response in 1950 than did Portage. The Bena plot, which was wet and has no history of defoliation comparable to the two plots just cited, yields a shoot development curve in 1950 comparable with the South Cass plot which was dry and heavily defoliated. The extreme shoot growth retardation at Portage, in view of the very high water levels artificially maintained through most of June, may be due mostly to inundation.

Many difficulties are encountered in interpreting data such as this. For example, expressing shoot length as percent of the preceding year's total is likely to be misleading since it can be shown in the case of Cass Lake, heavily injured for at least three years, that annual shoot length decrease due to injury occurs at a constantly decreasing rate. To express Beltrami shoot length as percent of the previous year's growth, which was already at a low level, is not the same as expressing Portage or Bena growth in the same terms. Only if all stands had the same history of attack would the resulting figures be comparable. The extremely low level of Portage elongation in combination with chlorotic foliage noticeable in August, 1950, gives reason to believe that high water could have been a factor in limiting oviposition in 1950. If, as we have reason to expect, adult emergence hit its peak by the first week of July when elongation was only 10 - 20 percent of the 1949 total, the adults would be confronted with shoots having egg capacities of 60.8 (top third), 22.4 (mid third) and 16.0 (bottom third). This is the condition that actually prevailed in 1950, whether due to flooding, previous sawfly injury, or both.

Effect of Inundation on Sawfly Larvae

One of the most spectacular examples of natural mortality to be observed during the two years in which this work was carried out was that caused by drowning of mature larvae. In 1949, rainfall during the first twelve days in July exceeded the 32-year average for Cass Lake by 4.49 inches. Occurring as it did, concurrent with maximum larval drop in at least one area of complete defoliation, the resulting ground pools within the cocooning universe were observed to contain hundreds of drowned larvae per square foot (Butcher, 1950).

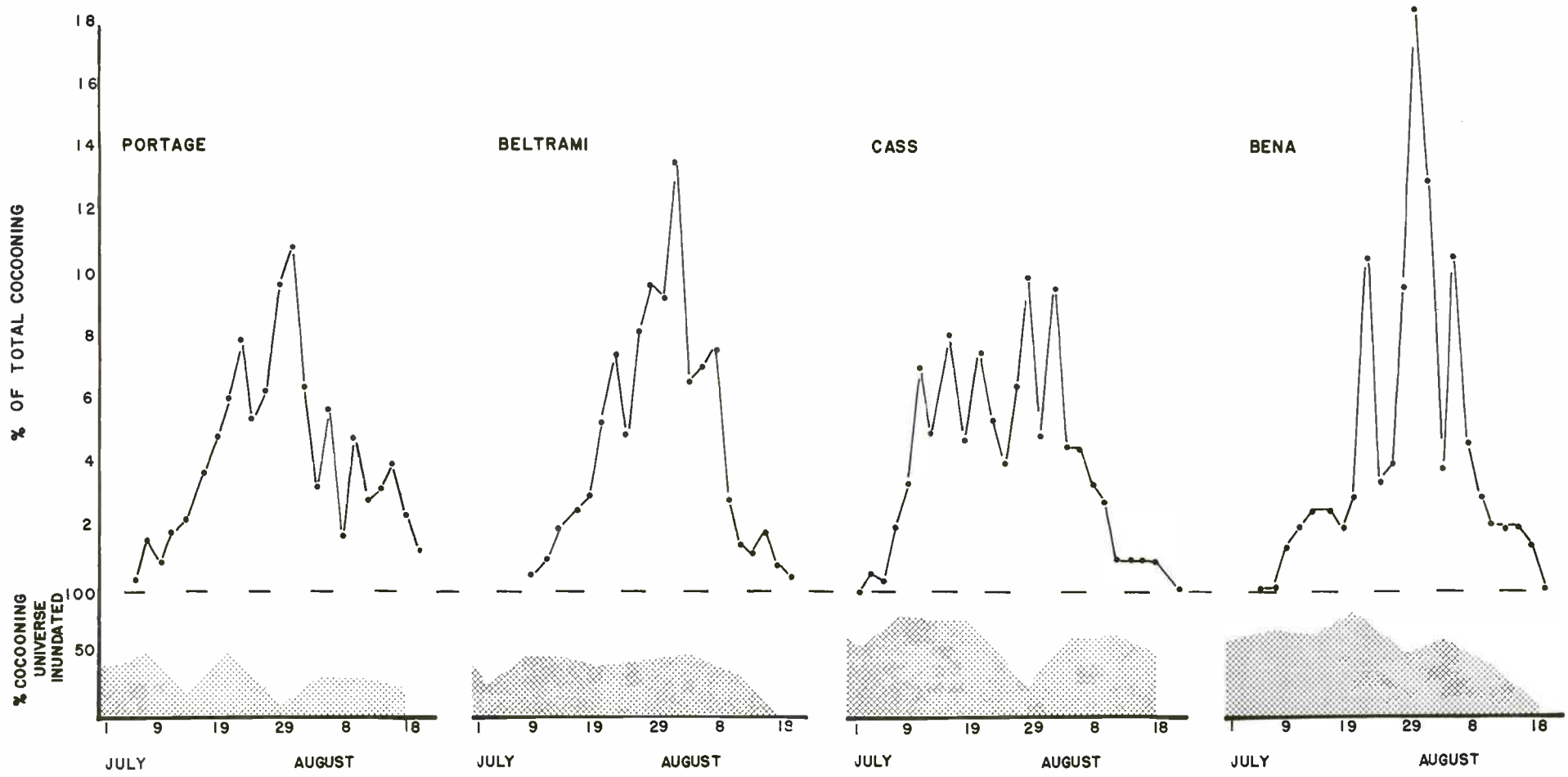
A further intimation of the importance of this study is suggested by work of Burbridge and Lejeune (1950), who found that susceptibility to flooding is greater during the "hardening-off" period than it is after the cocoons are 10 weeks old, tolerance increasing gradually up to that point, when they are able to withstand over 30 days' immersion. From this it would appear that many larvae leaving the tree, even if they were able to spin up in a suitable spot, would be susceptible to immersion if it occurred during the early stages of the "hardening-off" period.

Figure 7 illustrates the forest floor condition in 1950 for four study plots. At any given date, the likelihood of larval mortality due to drowning would be a function of the amount of surface water present. By dividing total frass production (dry weight) for each 48-hour period by the total frass production (dry weight) of an individual larva, an indirect estimate of the number cocooning at any given time can be derived. In Figure 7 these estimates are expressed as percent of the seasonal total cocooning in any 48-hour period for the areas studied. For example, if the numbers of larvae cocooning for any given 48-hour period per 8 square foot tray as deduced from total frass is accepted literally, on July 22 at Little Portage approximately 17 percent of those larvae dropping on that date could be expected to drown, since that is the percentage of the forest floor that was covered by surface water.

Heavy winds or rains, also, can cause many of those larvae not yet mature to drop prematurely, fifth instar larvae being particularly active and subject to dislodgement. If the data are accepted as a guide and not necessarily as an exact chronicle of events (all the details of which cannot be completely understood at this time) it is felt that this hitherto unrecognized source of larval mortality can be fairly accurately delimited.

Of more than passing interest are the differences in percent of cocooning universe inundation between the four stands pictured here, and a fifth not shown. The expression of cocooning as percent of the seasonal total for an 8 square foot vertical crown projection area does not convey the differences in the infestation levels that existed in these stands in 1950. It will be recalled that the Bena plot was less than 5 percent defoliated in 1950. How much build-up in this stand has been conditioned by a wet cocooning universe in past years can only be guessed at, but in 1950 it would not be unreasonable to assume that over 50 percent of the mature larvae in this stand were drowned before they had an opportunity to spin. In the South Cass plot, on the other hand, the cocooning universe was less than 10 percent under water from early June throughout the entire summer. This stand was completely stripped in 1950, and barring very high cocoon destruction by predators and unforeseen flooding in 1951, one could undoubtedly expect a repetition of complete defoliation in 1951. Populations at Cass, while relatively low in 1950, can be expected to remain at low levels in 1951 also. This stand drains into Cass Lake, but in 1950 the lakes were very high and remained so virtually all summer long, so that normal summer drainage into the lake did not occur.

Figure 7. Percent of cocooning universe inundated plotted with progress of seasonal cocooning.



Actual calculation of mortality due to drowning in this plot indicates that 57 percent of these larvae could be expected to have drowned in 1950.

The question that naturally arises at this juncture is: of what importance is 57 percent mortality in terms of the 1951 population? Is it really such a significant mortality after all? Using the Cass Lake specimen tree and figures on square foot cocoon counts, we can make a gross estimate of the potentialities of the residual population. Taking foliage volume at the 1950 level we can calculate the number of larvae necessary to defoliate the tree as follows:

$$\frac{\text{Total foliage dry weight}}{\text{Foliage Consumption per Larva dry weight}} = \text{Number of larvae necessary}$$

or:

$$\frac{567,530 \text{ mgs.}}{212.7 \text{ mgs.}} = 2,668 \text{ larvae}$$

Figuring a colony average as 65 larvae:

$$\frac{2668}{65} = 41 \text{ colonies}$$

In other words, 41 cocoons under a Cass Lake plot tree should, if given 100 percent progeny survival, be adequate for complete defoliation in 1951. Actually, as calculated in Table 4, accumulative frass collections indicate that a maximum of 19.5 larvae could be expected per square foot, assuming that all frass produced represents effective foliage consumption, i. e., foliage consumed by larvae which live to cocoon. Since 57 percent of these are expected to have drowned, actually only 8.4 larvae would be present per square foot, assuming further that no other natural mortality factors were operative. Multiplying this figure by 19.63 (the average crown projection area) the total per tree becomes 165 adults, or 4 times more than would be needed. If these figures are even remotely accurate, defoliation in 1951 will be on the order of 100 percent unless other agencies further reduce the population; this, in a stand which was only 15 percent defoliated in 1950.

It is not difficult, in view of the foregoing, to understand how populations of this insect could achieve epidemic proportions within a very brief period. The amazing fact that such outbursts are not more common emphasizes that many of the "brakes" on such increase are not yet understood. If further losses due to parasitism, predation by rodents, and mortality due to adverse overwintering conditions are subtracted, the picture is more understandable.

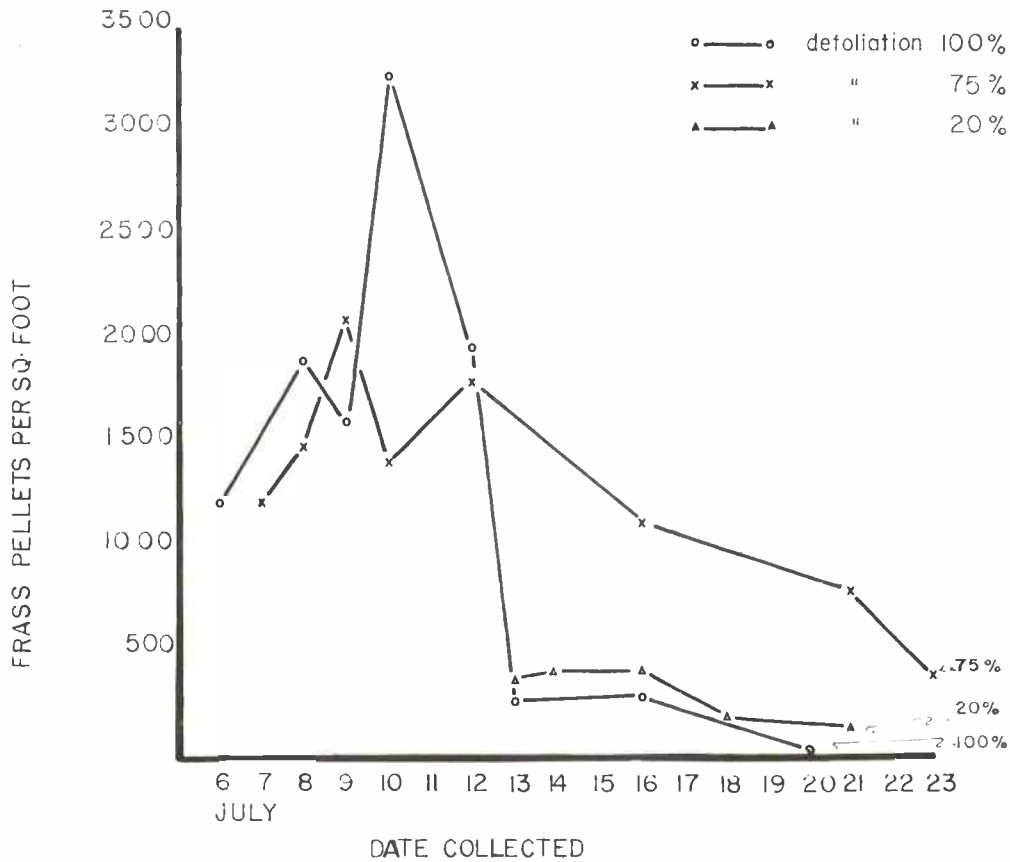
In 1949, for example, parasitism throughout the Lake States did not exceed 2 or 3 percent on the average. Rodent predation, a potential deterrent of considerable significance, can more properly be assessed in 1951 when quadrate cocoon counts are made of the cocooning universe in rodent exclusion cages currently in place. These will be compared with similar counts from adjoining quadrates of the cocooning universe to which rodents had free access. Some figures are available, however, (Graham, 1928) which attribute reductions of 50 - 80 percent to this agency, intensity of predation decreasing by site as the abundance and variety of herbaceous growth decreases. Further, this author found that from 30 - 100 percent of those larvae actually cocooning did not reach the adult stage because of unfavorable temperature, soil, or moisture conditions during hibernation.

One could indulge in pointless speculation beyond the data to show that the entire overwintering population might be wiped out by rodents or by adverse climatic factors. Each stand has its own characteristics, and both rodent predation and cocooning site suitability would vary from one stand to the other. Graham's figures were obtained by artificial caching, but one must assume that larva cocooning naturally will seek the most favorable sites, which would probably mean that moisture and temperature extremes would cause less mortality under natural conditions than were noted by Graham.

The preceding discussion of some of the data taken from literature and obtained from research tells only a part of the story. Accurate evaluation of catastrophes not ordinarily predictable is impossible, yet it would seem that these can be limiting factors under certain circumstances. For example, frass collections made in 1949 indicate that such phenomena as overpopulation can be catastrophic by leading to premature exhaustion of the food supply. In the stand referred to in the opening paragraph of this section, such a phenomenon occurred at the same time that torrential rains raised the water level to the point where 70 - 80 percent of the ground surface was inundated. Figure 8 illustrates the 1949 frass accumulation per square foot for three areas of various defoliation levels, the counts being equated to 24-hour values. The trees in the 100 percent defoliated plot were completely stripped of foliage by July 10, so it must be assumed that the larvae had to drop to the ground whether or not they were fully developed. Seventy to eighty percent of them dropped into the swollen ground pools and were drowned. Contrast this picture with that of a plot showing 75 percent defoliation, where feeding decline as evidenced by frass production was more gradual. This same pattern of feeding decline is apparent in the curve from a stand which sustained only 20 percent defoliation, only a portion of which is shown. It was not likely that comparable mortality occurred in the latter two stands, since dropping was delayed past the period of heavy flooding.

This example should also serve to illustrate the fallacy of long range prediction of sawfly abundance. Such effects are not only confined to mature larvae but also may be exercised on overwintered material. The preceding discussion of inundation is concerned only with larvae at the time of cocooning.

Figure 8. Frass production per square foot in stands of three defoliation levels.



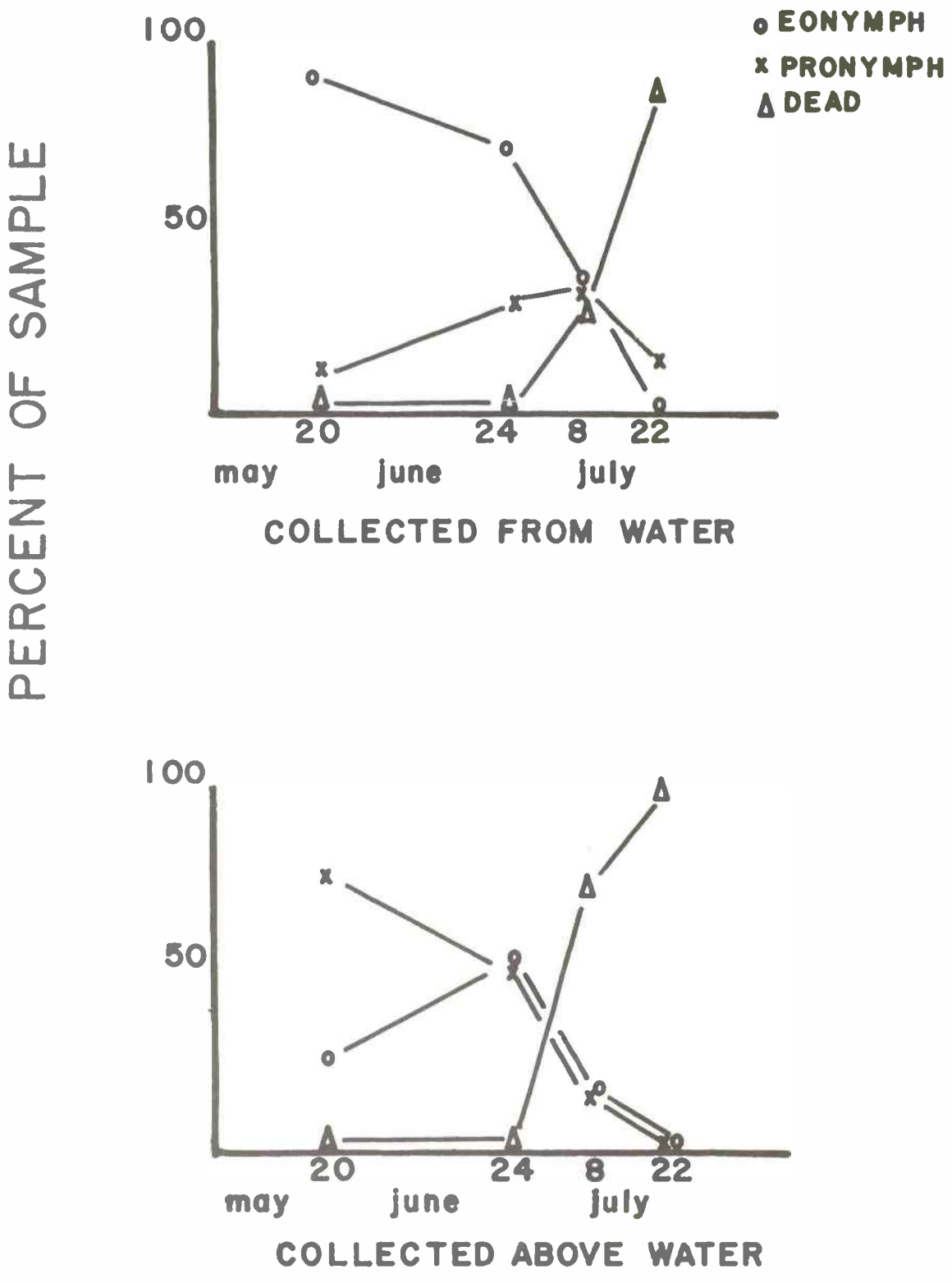
Effect of Inundation on Overwintered Pre-pupae

Lejeune and Piluk (1937) have considered developmental stages of pre-pupae and their relation to immersion. Their results indicate in part that "cocoons are resistant to submergence during the fall." The time of collection of cocoons used in these experiments is not stated, but in view of subsequent revelations by Burbridge and Lejeune (1950) the cocoons upon which most of the conclusions are based were at least 10 weeks old. Lejeune and Piluk found, in addition, that larvae undergoing metamorphosis in the spring and early summer succumbed more readily than did those which had not resumed development. Continuous submergence at this time, a condition which seldom occurs in the field, was found to result in complete mortality of larvae. They conclude that trees growing on "dry" sites were observed to experience little defoliation, those on "moist" sites the heaviest, and those on "wet" sites an intermediate degree of defoliation, generally speaking. These moisture levels are not further defined.

One phase of this work which was relatively untouched by the Canadian investigators involves the possible role of high water levels in prolonging development to the point where high temperatures apparently become inimical to survival. There are suggestions of its importance implicit in the findings of Lejeune and Piluk (1947) who report that the ratio of living to dead sawflies was high in those cocoons above water through June. By August this picture was completely reversed, all those above water having succumbed, while 5 percent of those intermittently submerged were still alive. These findings are supported by the following data obtained at the Little Portage Lake plot in 1950, where artificially prolonged high water levels provided an opportunity for similar studies. The procedure consisted of collecting 20 cocoons from above and 20 cocoons below water on each of the dates shown in Figure 9. Initially (May 20 and June 24) cocoons from above water were collected from the tops of hummocks. Because water levels were so high through June, these were the only spots not inundated. Subsequently, collections made on July 8 and July 22 were taken from soil which had been under water from late May through the third week of June and which was not again inundated. An attempt was made to select cocoons from those levels which were not covered with water when inundation reached 85 percent on May 20 and June 24. On July 8 and July 22 any soil not under water at the 70 percent inundation level was considered as a "dry" area. Collections from below water were relatively easy to make, since it was necessary only to search in the bottoms of the deeper pools to insure obtaining material which had been immersed continuously.

Each of these cocoons was dissected and the stage of development determined after the manner described by Prebble (1941) who described two main prepupal stages, eonymph and pronymph; the latter immediately preceding the pupal stage. Figure 9 shows how the pattern of abundance of each of the stages shifted under the dry as contrasted to the wet conditions. Adult abundance was greatest for the Cass Lake area on or about the first of July, and if the water levels had receded normally in the Little Portage plot, it is likely that the peak of oviposition activity in this stand would have occurred on or about this same time.

Figure 9. Pre-pupal development and mortality at Portage, 1950.



What seems to have happened, however, is that a rapid increase in mortality was taking place both in those cocoons above and below water. Figure 9 shows that 75 percent of those cocoons examined which were collected above water on May 20 contained pronymphs, while the remainder were still eonymphs. Those under water on May 20 were 90 percent eonymphs and only 10 percent pronymphs.

By June 24, of those collected above water, half were eonymphs and half pronymphs, indicating that over-all development was not proceeding at a rate comparable to emergence of adults. For those collected under water on June 24, pronymphs comprised 30 percent of the populations, an increase over May 20 of 20 percent. A concomitant and proportionate decrease in numbers of eonymphs was also in evidence at this date. By July 8 mortality began to show up in earnest, 70 percent of those cocoons above water containing dead individuals compared with 30 percent for those below water. By July 22, 100 percent of those above water that had not emerged were dead, as were 88 percent of those below water. Adult emergence from 3 cages (3 feet by 3 feet) covering naturally cocooned sawflies was on the order of 0.6 adults per square foot in this stand for the entire season. This represents a fraction of one percent of the cocoons present per square foot. The fact that no pupae were encountered in any of the samplings attests to the high mortality that was taking place. There is no question that some pupation was taking place, however, and the fact that pupae were not found is indicative of the error inherent in these small samples.

By way of aiding interpretation of these data a study of work done by Brown and Daviault (1942) is in order. These workers reared hibernating Pristiphora erichsonii larvae under 90 to 95 percent relative humidities and temperatures between 4 to 25° C. The highest survival was obtained among those larvae kept at 12 to 13° C. (54 to 56° F.). Even here, survival was on the order of only 30 percent, while at 61° F. survival was down to less than 8 percent.

Soil temperatures in degrees Fahrenheit at the insectary, Cass Lake (no canopy), were as follows on the closest date to the Portage collections for which information is available.

Time	May 30			June 24			July 7			July 21		
	Soil Depth in Inches											
of Day	12	6	1	12	6	1	12	6	1	12	6	1
8 a.m.	46	54	56	58	60	68	59	59	65	62	63	63
12 noon	46	54	60	58	68	74	58	65	69	62	67	70
6 p.m.	48	54	56	56	60	59	58	63	65	63	67	70

The temperatures at the 6- and 12-inch depths show only moderate diurnal fluctuations, so they are relatively independent of the effects of bright sunshine or clouds. The point to be emphasized is that by the last week in June soil temperatures probably were in excess of those found by Brown and Daviault to be most favorable for larch sawfly development. Low survival in this case may be attributed to other things than inundation itself. The results suggest that the long period of inundation may have delayed the development of the pre-pupal stages so

much that by the time they were released from immersion, temperatures were in excess of those that were optimum for development. The situation was complicated by the fact that the season was late and warm weather occurred more abruptly than is normal. Indeed, ten year phenological records from the southern part of Minnesota would indicate that this was so (Hodson, 1951).

STUDIES ON TREE DECADENCE

An important objective of these investigations was to determine, if possible, the history of attack in individual stands and the condition of each stand with respect to sawfly induced decadence. Although the ability of tamarack to withstand up to three 100 percent defoliations under certain conditions (Graham, 1931; Craighead, 1940) has been reported, prior to 1949 the history of defoliation in any particular stand was not known. In order to act intelligently to minimize loss of trees heavily injured before 1949, it was considered necessary that the oviposition attack histories be properly interpreted, particularly since manifestation of decadence through increment loss presents problems of interpretation (Graham, 1931) which limit its usefulness as a working formula for anticipating mortality.

In his studies of defoliation, Graham (1931) performed experiments on trees which were five years old at the time of first defoliation. Hand defoliations of 25, 50, 75 and 100 percent were carried out at the time defoliation by the sawfly was taking place in the field. The respective trees were defoliated in this manner for four successive years. It was found that all of the completely defoliated trees put forth foliage after three consecutive strippings and two out of ten trees had a few needles and a small amount of green cambium left after four strippings. Those trees only partially stripped outwardly showed little evidence of injury after four years, although those defoliated 75 percent for four years showed somewhat thinner foliage than did those in the control. On the other hand, dry weight of needles per fascicle at the end of the 4-year period was shown to have declined in proportion to defoliation severity.

As regards the effect on increment, growth increased significantly the year of defoliation in the case of those stripped of all foliage, whereas the reduction in other trees was proportionate to the degree of defoliation. Increment fell sharply in the second year of complete defoliation, but continued to increase at rates inversely proportional to defoliation in the others. In the case of complete defoliation, Graham states that increase in increment shows up in the basal sections while the upper sections show little increase, and may show an actual reduction the first year of defoliation.

The results of this work contribute greatly to our knowledge of how tamarack reacts to sawfly defoliation. We still do not have enough information, however, on the effects of defoliation on trees growing on different sites, nor do we know for certain that trees in all age classes will react in the manner described by Graham. Also, is defoliation of 100 percent followed by lesser degrees of defoliation going to cause mortality eventually, or will the trees continue

to subsist at low levels of vigor and ultimately respond to release of defoliation pressure by resuming normal growth? What seems most important of all is the question of how much has the vigor of infested stands declined because of the current outbreak, and what criteria of decline are available upon which risk estimates may be based?

Under field conditions it seems unlikely that defoliation will persist at the 100 percent level for several years in succession. It seems more likely that starvation of larvae, predation of cocoons, and climatic catastrophes, to mention a few factors, would tend to make populations fluctuate from year to year. Under these circumstances, information on the effects of 100 percent defoliation four or five years running are useful but not necessarily indicative of what happens in nature. In the final analysis, it is the effect of what has actually taken place that must form the basis for action programs. To this end, various manifestations of decadence were investigated for the light they might shed on possible tree mortality.

Extent of Previous Injury

Fortunately, estimates of the relative density of sawfly populations in preceding years were possible from detailed counts of shoots injured by oviposition in those years. Detection of any particular year's terminal growth is relatively simple, since the needle fascicle base exhibits a perceptible annulus for each year of its existence, and the shoot deformed by oviposition is recognizable up to five years later.

Oviposition intensity was determined in the following manner. In 1950 five trees were selected from each stand and a primary branch from the top, mid and bottom crowns taken from each. Total numbers of new shoots for each of the years 1947, 1948 and 1949 were counted, along with the number injured by oviposition in each of these years. Through an inadvertent omission, total number of shoots present in the 1947 sample was not recorded for the Cass plot; otherwise the data is complete for all five study plots. It is felt that the data are adequate to convey the population levels as they existed in 1947-1949. Table 10 lists the total numbers of shoots and total and percent injured in the respective years.

Table 10. Percent of Total Available Shoots Injured in 1947 - 1949

Study Plot	1949		1948		1947	
	Total	Percent Injured	Total	Percent Injured	Total	Percent Injured
Cass	607	49.3	1423	69.9	--	--
Beltrami	916	35.6	586	6.1	182	1.1
Portage	1402	9.8	718	12.8	267	0
S. Cass	1263	7.4	635	6.9	390	1.0
Bena	1336	2.4	401	0.3	156	0

These data are graphed in Figure 10, where each plot is shown with the percentage of shoots injured 1947 - 1949.

From these data the following picture of probable past defoliation can be constructed.

Table 11. Probable Defoliation 1947 - 1949 in Five Study Plots Based on Oviposition

Study Plot	Heavy 50 percent			Moderate 20 - 49 percent			Light 6 - 19 percent			Very Light 0 - 5 percent		
	47	48	49	47	48	49	47	48	49	47	48	49
Cass	x	x	x									
Beltrami			x		x			x				
Portage					x	x					x	
S. Cass					x	x					x	
Bena									x	x		x

The picture of previous defoliation as derived from oviposition attacks in the respective years is offered not merely as a preliminary to the interpretations that follow. It also has value as a method of interpreting population history.

Because this phase of the study is essentially exploratory, the extent of the sampling and the manner in which it was carried out may be open to question. Undoubtedly there is considerable room for improvement, particularly in regard to the size of the sample. The interpretation of decadence to be presented, however, would seem to indicate that these results accurately reflect the defoliation histories of the respective plots.

Shoot Length as a Manifestation of Decadence

The significance of shoot length as a deterrent to sawfly build-up was discussed at some length in a preceding section. It would also appear that valuable information on tree decline might be forthcoming from comparisons of data between various study plots for which oviposition records were available. Since sources of shoot length variation due to other factors such as seasonal growth peculiarities or local site conditions are recognized, a comparison of shoot lengths between two trees in two different stands is obviously without meaning. On the other hand, comparisons of the same shoots from the same trees from one year to the next tend to give a better control over these variables, and a dependent relationship with other phenomena, if established, would seem more credible.

In pursuing this line of investigations, uninjured shoots of 1948 and 1949 growth were measured at the three crown levels. Ten 1948 and ten 1949 shoots were measured from each of three branches from five trees in each plot. Interpreting data from the Bena plot as representative of the condition obtaining in an "uninjured" stand, the various plots would be expected to follow the same pattern unless some other factor was operating to alter the picture. If, as it

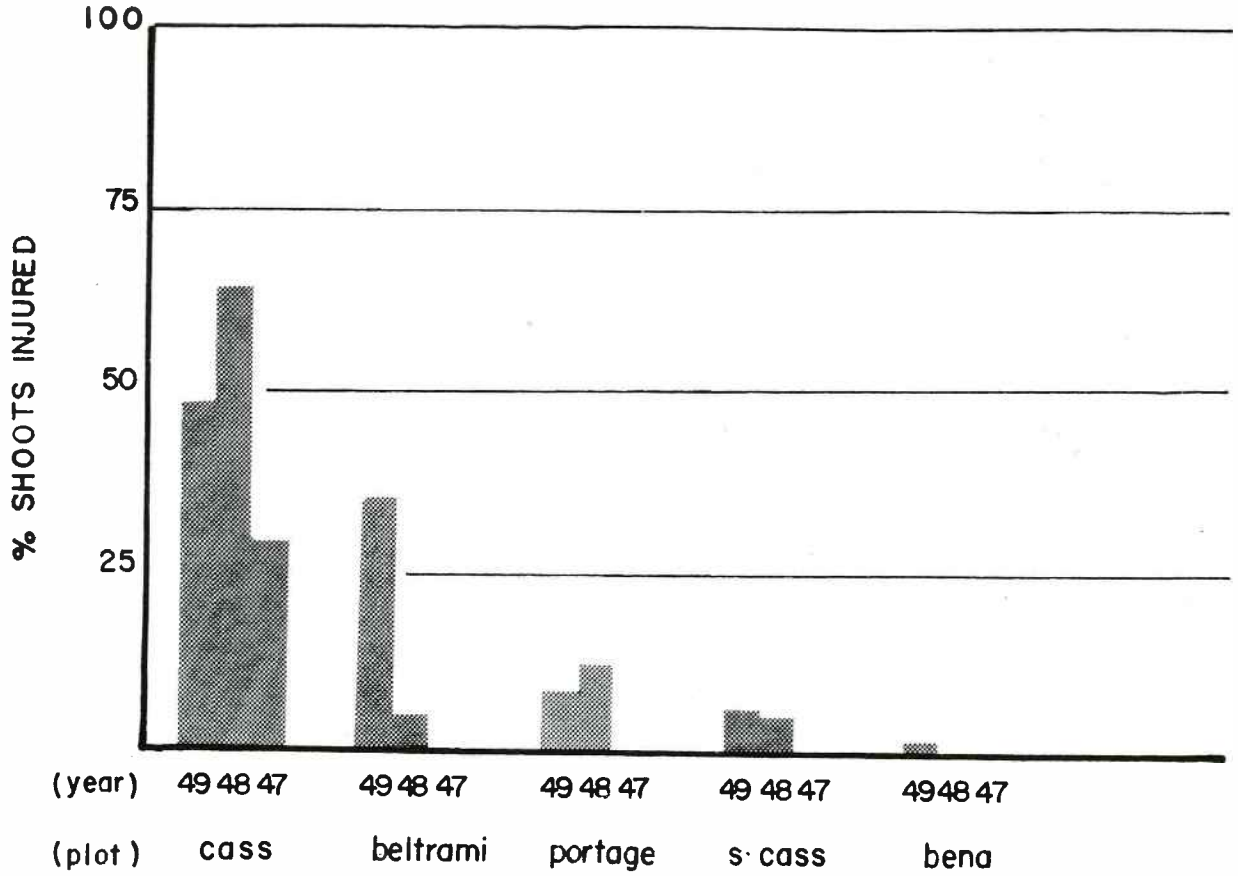


Figure 10. Percentage of shoots injured by oviposition in 1947, 1948 and 1949 on 5 study plots.

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actually developed, departure from the Bena pattern is of an order consistent with degree of oviposition in previous years, there is good reason to suspect that the differences are due to the sawfly. Figure 11 illustrates shoot length in centimeters for the years 1948 and 1949 in the five different plots. Averages of 50 measurements are depicted for each point and at three different crown levels. Note that Bena averages are almost identical for 1948 and 1949. Note, too, that while the departures from the Bena position are not great in the case of three of the plots in 1948, they are increasingly so in 1949. Furthermore, the Cass Lake plot shows consistently large departures from the Bena configuration in both 1948 and 1949. In interpreting these results it should be remembered that no attempt is being made to ascribe shoot length decline to oviposition alone. Oviposition injury merely provides a means of determining sawfly populations and consequent defoliation. The reduction in shoot length is undoubtedly due to a combination of oviposition and defoliation effects.

By comparing this picture with the infestation levels described earlier for the various stands the association seems clear. In 1948 the Cass plot trees were heavily attacked, as Table 11 indicates. Although a relatively small departure from the Bena configuration is evident in the case of the other three stands in 1948, the figures show that considerable oviposition took place in all. In 1949, on the other hand, the departure from the Bena curve is high in Beltrami and Cass and considerably more for the S. Cass and Portage plots than it was in 1948. The positions of the S. Cass and Portage levels in 1949 are not consistent here, but this is probably due to sampling error.

A further elaboration of these data, this time including only those measurements from the top third of the respective crowns, is presented in Figure 12. The data for the top third of the crown is presented separately because it follows that in a well-stocked stand this is the most actively growing region of the crown and should be least influenced by crowding and shading. Here, simultaneous plotting of shoot lengths (bar) for the five areas and percent of total shoots injured (line) shows the apparent relationship of shoot length to oviposition injury.

Figure 11. Shoot lengths at various crown levels in five study plots.

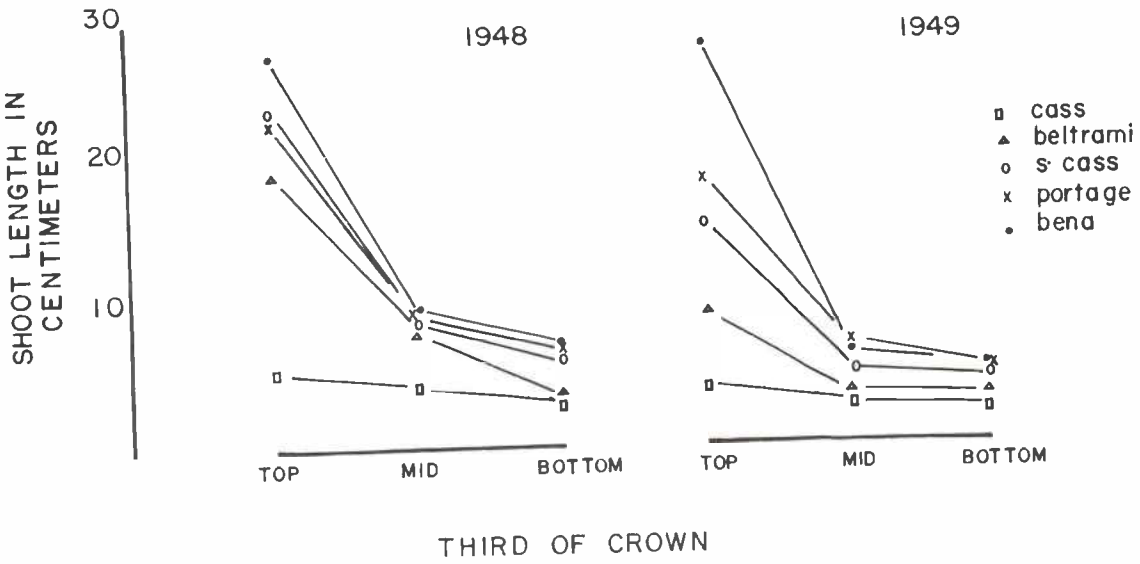
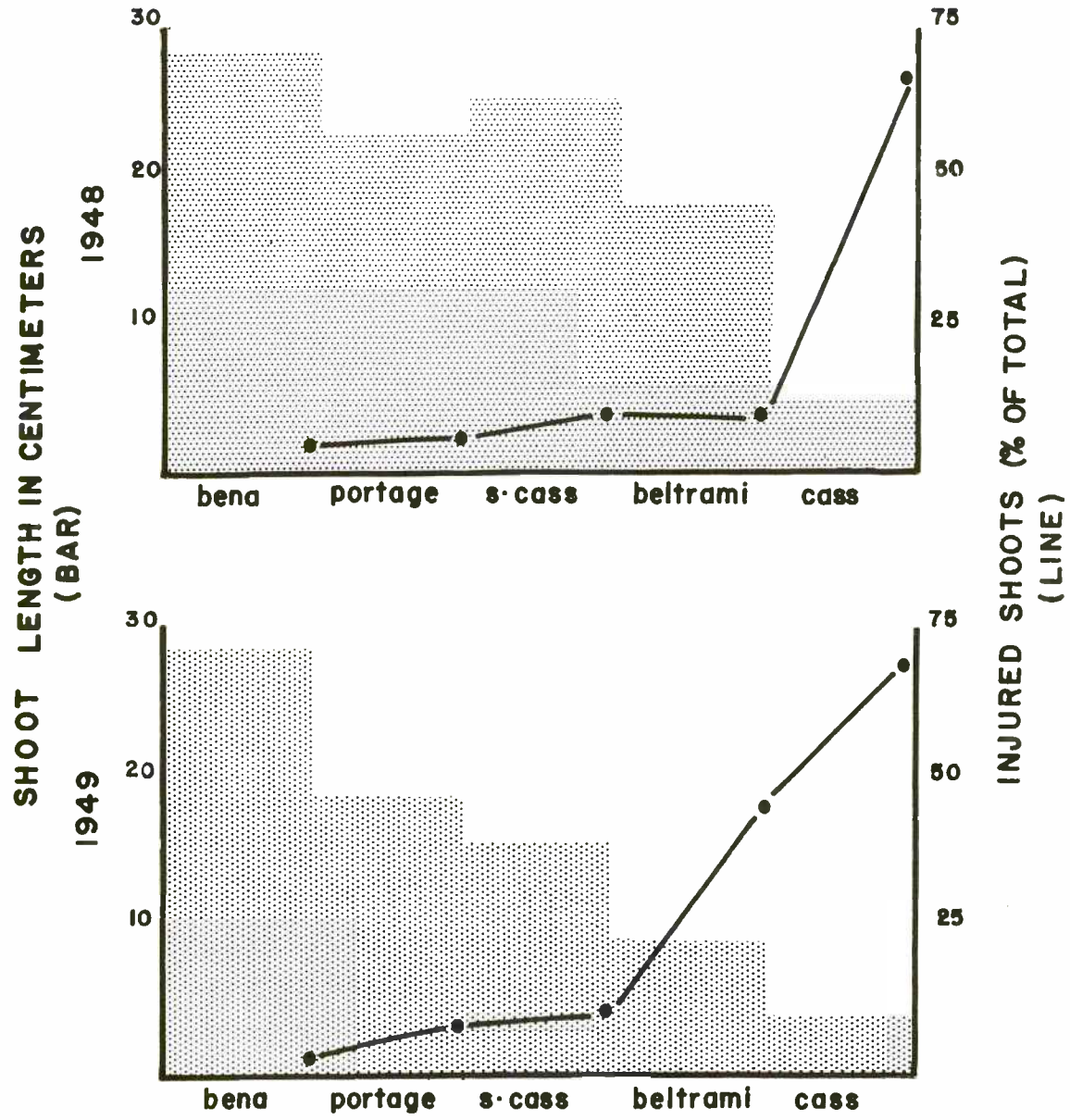


Figure 12. Relation of oviposition injury to shoot length.



In the preceding graph, those stands showing the least oviposition attack display longer seasonal shoot growth than do those which are hit more severely. The relationship approaches reciprocity in 1949.

It is worth mentioning that Graham in his work (1931) did not call attention to any such symptoms of decline except to point out that needles were smaller on individual defoliated branches, and that heavily defoliated branches died back at the tip; or, as in one instance, died back completely. Branch die-back, however, cannot be considered a useful criterion of decline caused by sawfly unless there is good reason for attributing it to the insect. In many cases it is possible to observe this condition in the absence of oviposition injury, particularly at the lower levels of the crown.

The pattern of shoot length decline as presented here could have practical value. For example, any method of direct control for this insect must be on a selective basis. Further, at the present time land managing agencies cannot afford protection spraying of tamarack which is primarily designed to prevent loss of increment. The decision of when to spray for sawfly control must be based upon the knowledge that such spraying is necessary to prevent tree mortality. Because tamarack is scattered over such a large area, and Forest Insect Laboratory personnel are consulted by county and state officials in regard to infested tamarack which they supervise, decisions as to the vigor of particular stands must be made on the spot. If it were possible to observe the progress of infestations in such stands from year to year, the information which we now have as a result of Graham's (1931) and Craighead's (1940) work would probably provide a basis for recommending action. Since we do not have this opportunity, it becomes necessary to make decisions on the basis of the facts as they may be interpreted from oviposition injury and decadence symptoms.

By way of interpreting the data in Figure 12, attention is directed to the percent of shoots injured and the shoot length for the Cass plot. It will be recalled that this stand sustained heavy defoliation as early as 1947. While information on shoot length for 1947 is not available, it is evident that the 1949 length declined very little over 1948. In other words, in this particular stand, shoot length appears to be decreasing at a decreasing rate. It is possible that the lighter attacks in 1949 (75 percent defoliation) gave these trees a respite which prevented mortality; but the fact that shoot length was not much less in 1949 than it was in 1948 suggests that there was a leveling off in tree vigor. If even this were known in 1950, and if information from cocoon counts had indicated a high population of sawflies, the recommendation would have been made that this stand be sprayed to prevent possible mortality.

Assuming that trees in all these stands will react in the same manner as did those in the Cass plot, it seems unlikely that any of the other stands would exhibit mortality in 1951 regardless of the populations present in 1950. Using this reasoning, a selective control program would reject control in these stands until the following year at least.

Decline in Shoot Number as a Decadence Manifestation

Numbers of new shoots per primary branch at Bena increased in the manner shown in Figure 13 over the period 1947 - 1950. If it is assumed that this pattern of shoot addition is normal for stands in this age class, numbers for the other stands can be considered abnormally reduced in the degree illustrated. These figures were obtained from top branches only and represent total new shoots for the respective years from 5 top branches in each stand. By comparing the position of the curve in 1947 and 1948 there appears to be little difference in total numbers in any of the stands. By 1949 the deviations from the Bena curve are achieving the same order as did the shoot length measurements. By 1950 the pattern is more clearly defined and is in good agreement with the departures exhibited in the shoot length graph (Figure 11) and the order expected on the basis of oviposition injury (Table 11).

Figure 14 shows numbers of new shoots expressed as percent increase in numbers of new shoots (line) plotted against percent of shoots injured (bar) for the 1949 over 1948 and the 1950 over 1949 periods respectively. These are figures from top, middle and bottom branches from each of the 5 study areas.

The consistent correspondence of these phenomena with oviposition injury suggest that the latter injury and defoliation affect the size and number of new shoots in a degree proportionate to their severity. One would not expect a decline in numbers of new shoots to be nearly as accurate a reflection of the reduced vigor which follows defoliation, as shoot length reduction. Many of the shoots injured by oviposition do not respond with fresh growth the following year, although a surprisingly large number do. Nevertheless, a large part of the reduction in shoot numbers appears to be a consequence of heavy feeding; and to that extent such a numerical decrease is symptomatic of general decline in vigor.

Needle Size Reduction in Relation to Injury

Of possible significance in anticipating tree mortality is the relationship of needle size at the top, middle and bottom portions of the crown. Data based on one tree from each of the Bena, Beltrami and Cass plots give the picture shown in Figure 15. Here the dry weights of 10 fascicles from each of the top, middle and bottom crown thirds are plotted for each stand. The Bena curve gives the impression of more luxuriant foliage at the top third of the crown; with the middle and bottom thirds less so. Beltrami needles show this same pattern but at a lower level. Cass needles, on the other hand, are smaller on a dry weight basis at the top of the tree than they are at the bottom; a complete reversal of the Bena configuration. It is known that the Beltrami foliage was completely removed in 1949 so that all of the 1950 needles may be assumed to be growing on branches completely defoliated the previous year. Cass, on the other hand, was not completely stripped in 1949, but was very nearly so. Probably the bottom foliage of the sample tree was not removed in 1949, but that from the top and the middle was.

Figure 13. Pattern of shoot number increase, 1947 - 1950.

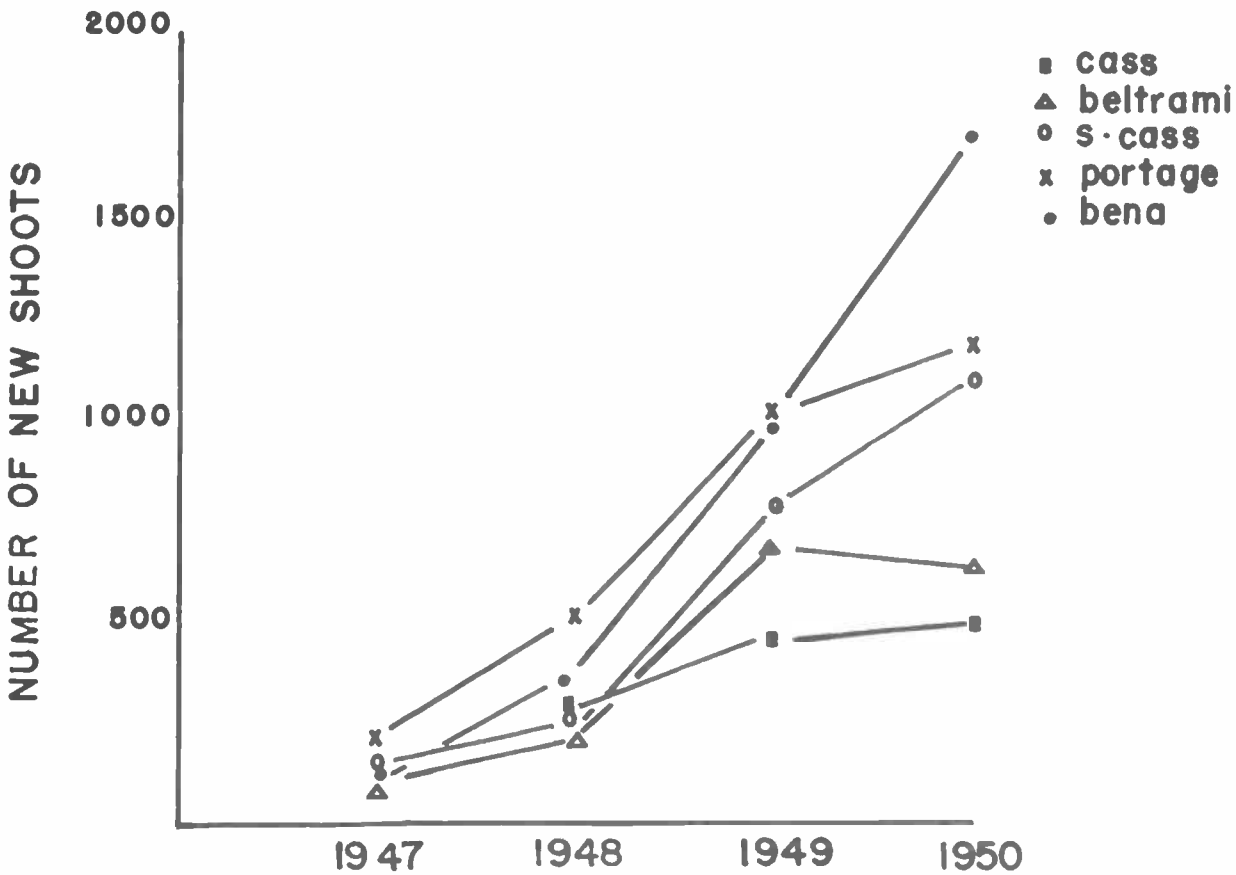


Figure 14. Number of new shoots per top, middle and bottom branch plotted against percent of total shoots injured.

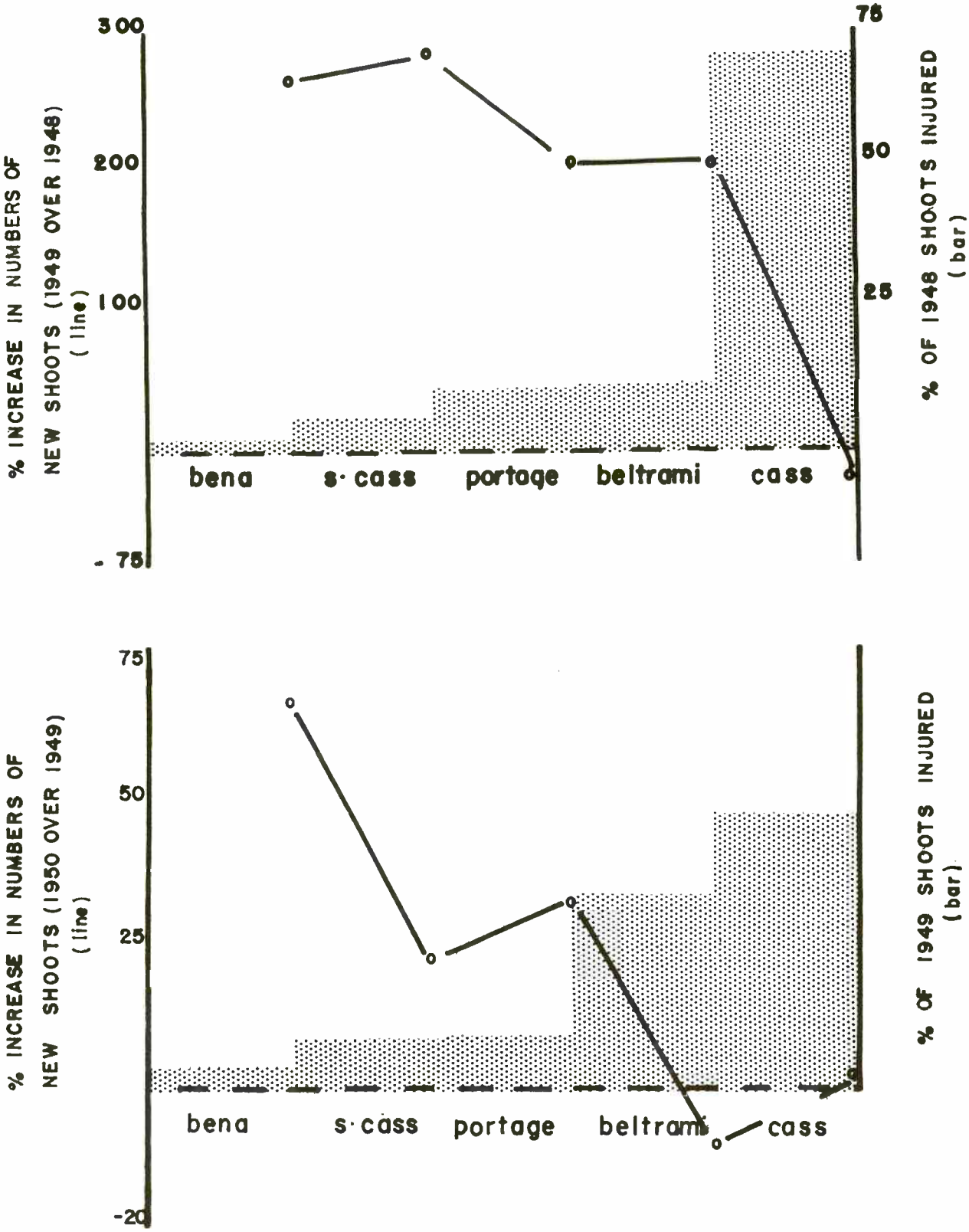
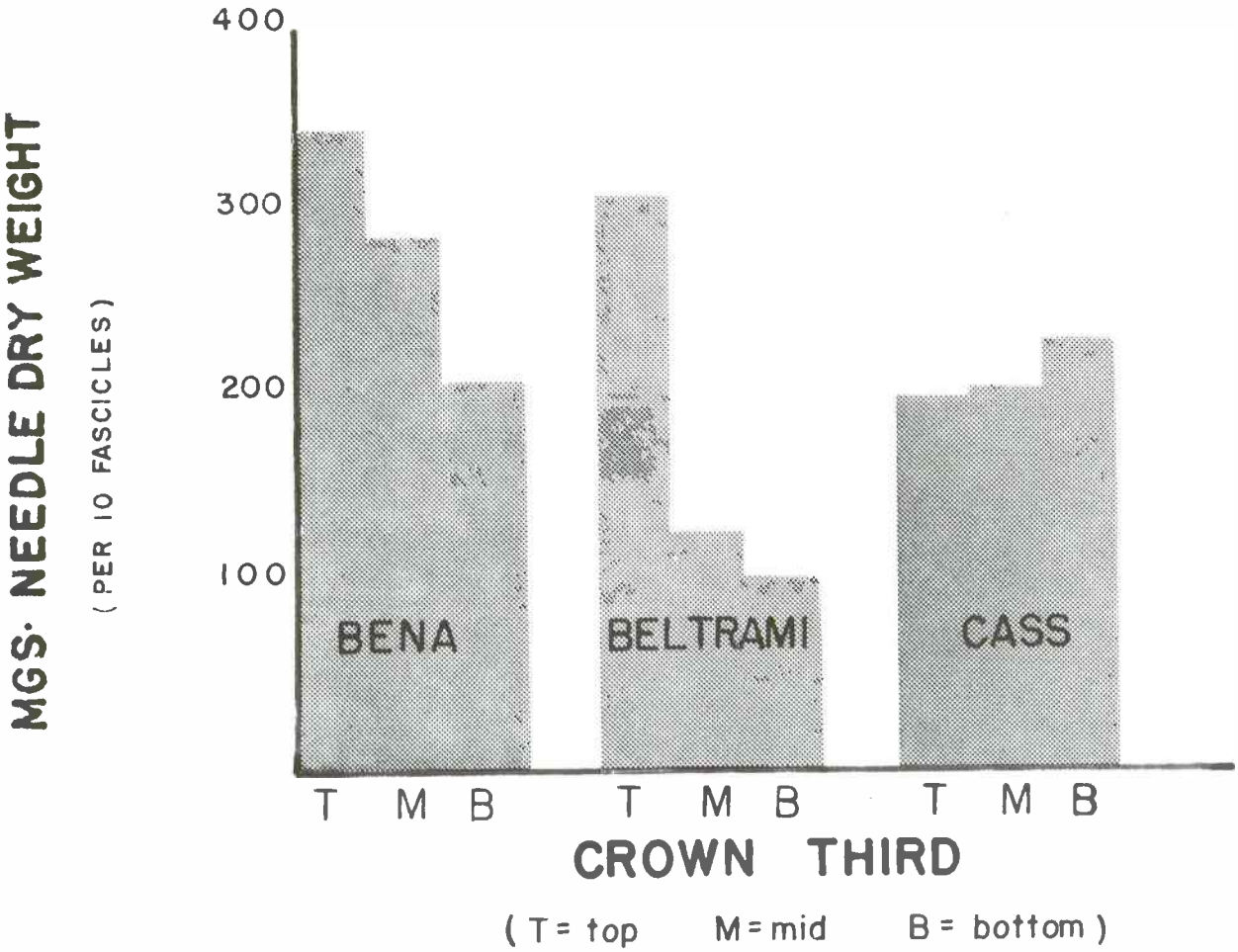


Figure 15. Relation of needle size to position on crown for trees from three plots.



A sensible interpretation of this picture is impossible, except to point out that the position of the Beltrami curve at a lower level than that of Bena in 1950 is probably a consequence of the heavy defoliation it experienced in 1949. It must be assumed that foliage characteristics of the two stands were similar before injury. The Cass curve, being both lower and of a different shape than that of Bena might be interpreted as resulting from repeated heavy defoliations which were not always 100 percent.

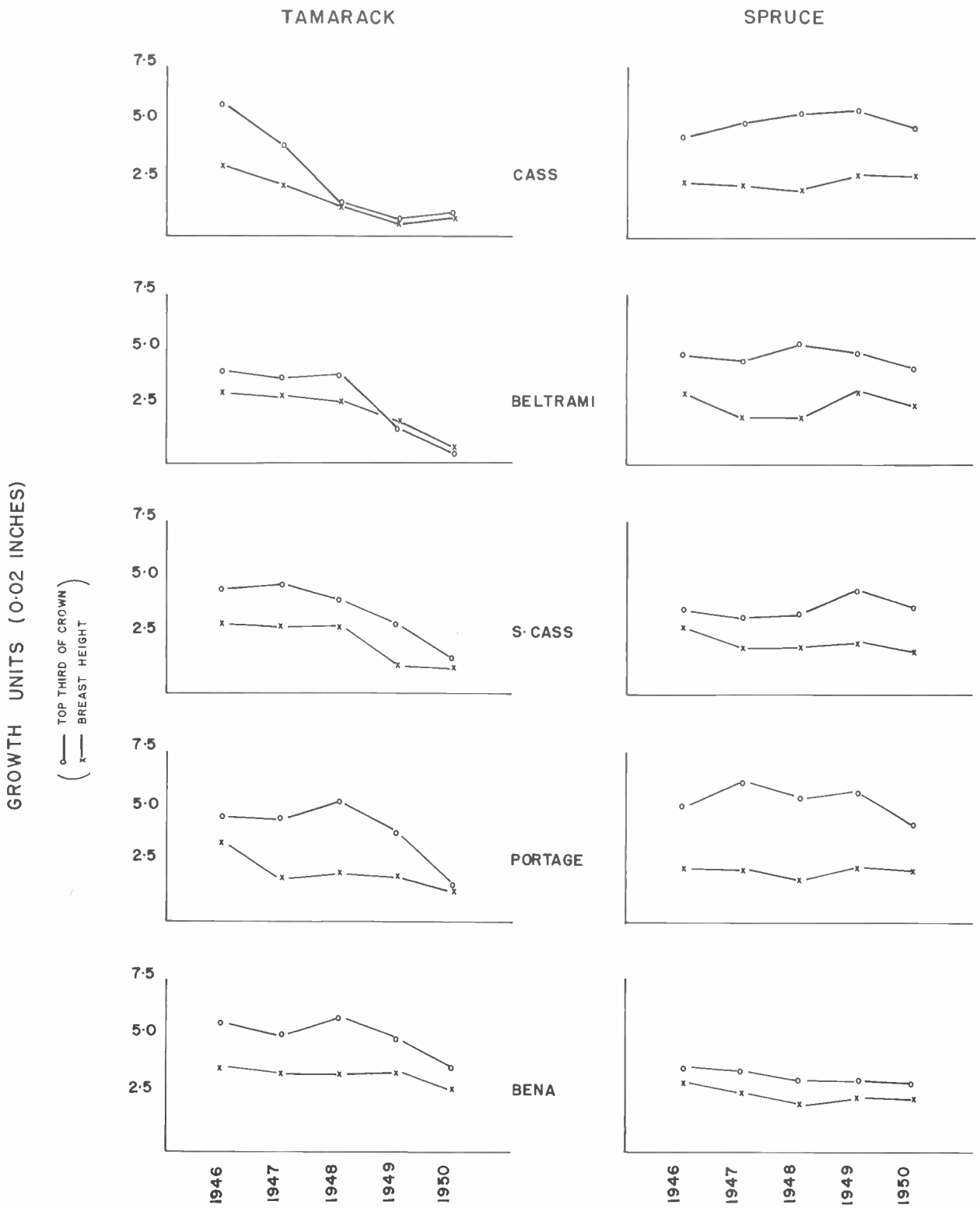
Further work along this line should clarify this picture somewhat, but in the meantime there is no disposition to attach much importance to the data.

Interpretation of Increment as Evidence of Decadence

Graham (1931) in his studies of tamarack growth found that basal sections revealed an abnormal increase in increment for the year of defoliation while sections from the top of the stem showed no such increase; on the contrary an actual decrease was observed in some instances. The work of this author would seem to rule out the interpretation of increment as a measure of sawfly defoliation in the early stages of an infestation, particularly if the readings were made from basal cuts. In order to substantiate these findings 5 co-dominant tamarack trees were selected for cutting from each of 5 study plots. Sections were cut from (1) the top (4-1/2 feet down); (2) the middle of the stem; (3) 4-1/2 feet from the ground and (4) 1 foot from the ground. Similar cuts were made from 5 co-dominant black spruce (Picea mariana (Mill.) B. S. P. from each stand and comparisons made. Figure 16 illustrates reduction of radial increment in the 5 stands at the top and at the 4-1/2 foot level. Each unit represents 0.02 inch and the figure for any year at each level is an average of 4 measurements per section based on 5 co-dominant trees per stand. Contrary to expectations, the stands were not completely even-aged. At Bena, for example, 2 out of the 5 trees cut were 63 years old, while the remainder were only 32 years old. The older trees were definitely in the minority. The fact that co-dominants were selected make it seem likely that if any older trees were present, they would be represented in the sample. The older trees appeared to be putting on more radial increment than the younger where they occurred together, but appeared proportionately affected by defoliation for the most part.

From the data presented in Figure 16 it is questionable whether measurements made at the top of the trees reflect insect injury any sooner than do measurements made at the 4-1/2 foot level. The accuracy of such comparisons is compromised by the greater magnitude of growth and consequently the larger size of the fluctuations at the top portion as compared to the bottom, presumably in response to other growth influences. Percentage-wise, increment reduction in the Cass plot is consistently greater at the top than at the bottom; in keeping with the trend exhibited by other manifestations of decadence as regards degree. This is also true for trees from the other plots but the superiority of top measurements as an indicator of intensity of attack over similar measurements made from sections of the lower portions of the stem is questionable on the basis of these data.

Figure 16. Radial increment of tamarack and spruce on five study plots for the period 1946 - 1950.



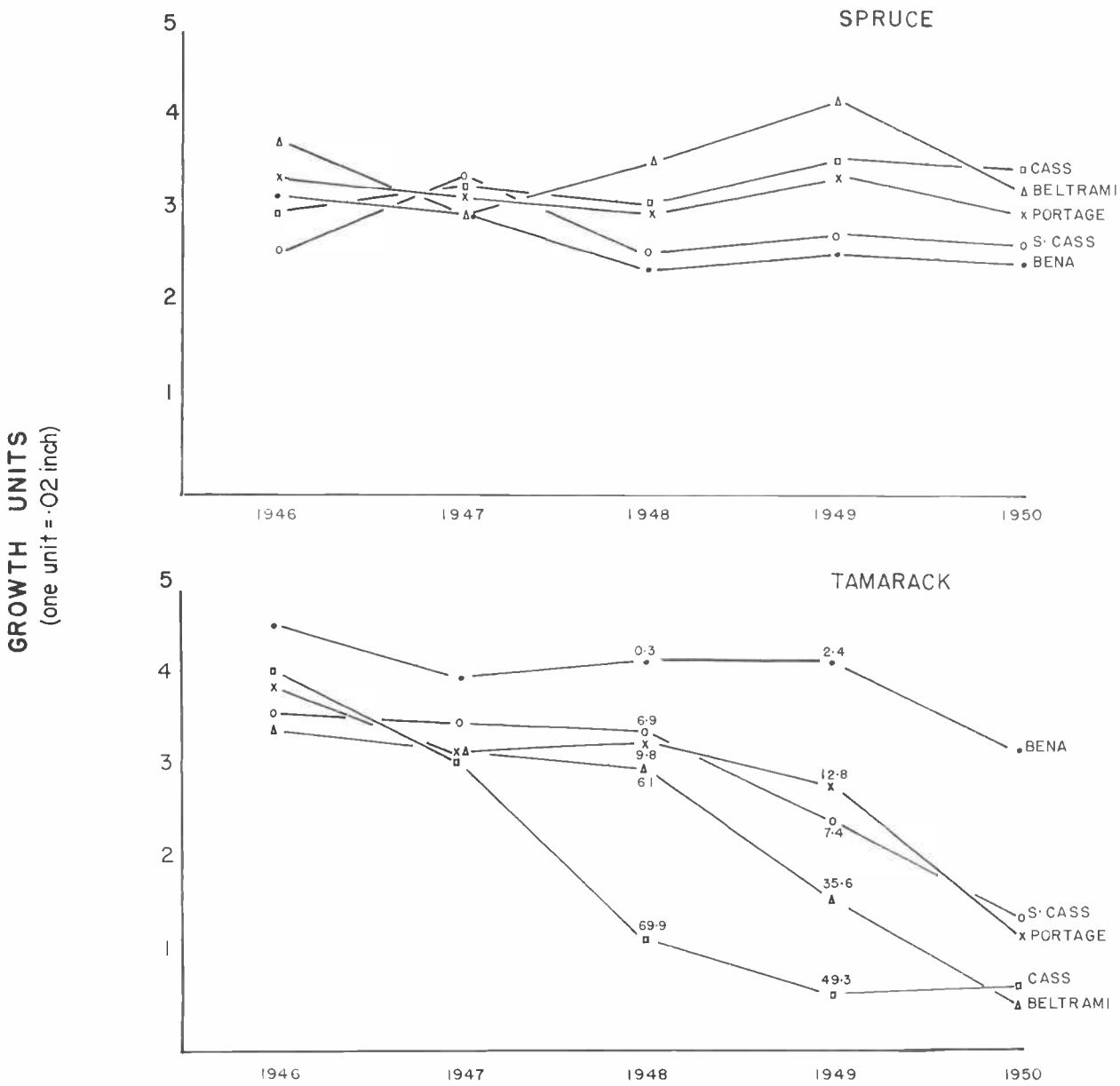
The chief objective of these radial growth studies was to determine the pattern of increment reduction resulting from sawfly injury. A figure for average annual increment per tree was obtained by taking the average of all four sections per tree for each year; the measurements per section being made in the manner described in the first paragraph of this section. The results of these measurements are summarized in Figure 17.

It was hoped that these data would afford a check on the accuracy of shoot length, shoot number and needle size as indicators of tree decline. Since it was impossible to have controls of uninjured trees in the same stands as those that were infested; black spruce, a species not affected by the sawfly or at present significantly defoliated by any other insect, was handled in the same manner for purposes of comparison.

An examination of the curves for tamarack in Figure 17 indicate that the departure from the Bena curve conforms to the pattern expected on the basis of counts made of injured shoots for the respective years (Table 11). Also, the rate of decline complies with severity of defoliation in the respective stands, and the position of each curve (i.e. the magnitude of increment loss) is in excellent agreement with those exhibited by the curves for shoot length (Figure 11). That these alignments for the respectiveplots are not due to differences between areas that are unrelated to insect attack is further demonstrated by the general uniformity of the curves for spruce, also shown in Figure 17. The lowest curve for spruce is that of Bena whereas the exact opposite situation exists for tamarack. The Cass increment dropped consistently from 1946 - the first year of heavy defoliation. It follows that the low level to which increment in this stand had dropped in 1949 made it unlikely that anything but an increase or mortality, could occur the following year given a respite from defoliation such as occurred. The reductions at Portage and S. Cass beginning in 1948 are in keeping with the severity of attack as evidenced by oviposition injury for the respective years. Apparently, if 5 to 10 percent of the shoots were injured, defoliation was appreciable, and this is reflected in increment decline from 1948 on in 4 of the 5 plots.

With this information and that which preceded it, a fairly reliable estimate of the history of the current epidemic is possible. The fact that old injury is apparent from oviposition scars and that, within limits, criteria of decadence are available which accurately reflect previous injury promises to provide a useful approach to selective maintenance control. This information can provide a working basis for anticipating mortality, and, most important, should eventually yield information as to when control measures must be instituted in order to forestall tree mortality.

Figure 17. Annual radial increment of tamarack and black spruce for the years 1946 - 1950.



SEASONAL DEVELOPMENT AND ITS SIGNIFICANCE IN CONTROL

This section is concerned with attempts at translating information on biology into a workable approach to control. From the discussion of life history presented at the beginning of this paper, several aspects of sawfly biology would seem to make effective control of this insect by chemical means impossible. Two things that seemed insurmountable if control was to be effected by one spray application were (1) the prolonged period of oviposition activity, and (2) the fact that larvae have been reported to hold over in the soil for 2 or more years. Each of these habits, if of sufficient importance, could conceivably be capable of insuring survival of a residual population even if complete mortality could be achieved of all those adults and larvae present on foliage at the time of spraying. The discussion which follows offers some provocative and unexpected information bearing on these problems.

Association of Adult Emergence with Frass Production Peaks

In order to determine just what the seasonal pattern of adult emergence was like in 1950, eight 3' x 3' x 1' cages were placed in 4 plots as follows: 3 at Portage, 2 at Beltrami, 2 at Cass, and 1 at S. Cass. Each of these cages was covered at the top and sides with 16 mesh copper wire screen. The open portion was countersunk approximately 8 inches into the cocooning universe, so that a 9 square foot surface was covered by each cage. When adults were observed within the enclosure the entire cage was lifted; the insects were counted and placed in a collecting jar. Except on very warm days the adults were sluggish and easily caught. At any time, counting was relatively simple.

It was hoped that by this method the emergence of adults under natural conditions could be determined. It should be emphasized that the sawflies in the soil had cocooned naturally; they were not cached. In the Beltrami plot, for example, the 3 trays upon installation in early May were placed - one over a deep ground pool, the second straddling a shallow ground pool and low hummock, and the third over a high hummock which was not under water at any time during the spring and summer. At the South Cass plot the one cage used was placed over the cocooning universe on high and dry ground. As previously mentioned, this particular plot was less than 10 percent inundated at any time during the season. The two cages at Beltrami were placed on elevated ground, as were those at Cass. In view of the fact that all of these areas were heavily defoliated in 1949, and cocoon populations in all of the areas were substantial at that time, it was felt that enough sawfly adults would be forthcoming to give a picture of the pattern of emergence. Figures of total adult emergence for the season for the 4 plots sampled are as follows:

Table 12. Emergence of Larch Sawfly Adults from 3' x 3' x 1' Cages for 1950 Season

Plot	Number Cages	Cocooning Universe Covered (Sq. Ft.)	Total Adults
Case	2	18	5
Beltrami	2	18	1
Portage	3	27	16
S. Cass	1	9	40

These figures seem surprisingly low, despite the fact that the cages were examined every 48 hours after installation and the improbability that any sawfly adults were missed. By way of a check, however, it is of interest to digress and reconsider what could have been expected per square foot in view of actual defoliation in 1950. Using the Case plot as an example where emergence from 2 cages covering 18 square feet was 5 adults; if the number emerged is divided by the number of square feet, a figure for total adults per square foot is obtained. In this case emergence was at the rate of .28 adults per square foot.

Average foliage consumption per tree in this stand in 1950 was 81,242 milligrams dry weight (see Table 4). It was determined through rearing that an individual larva consumed 212.7 milligrams dry weight of foliage. By dividing this figure into 81,242, the following estimate of number of larvae actually completing development is possible.

$$\frac{81242}{212.7} = 381 \text{ larvae per tree}$$

This figure of 381 larvae can be useful if it is assumed that all the frass upon which it is based was from larvae which actually reached maturity. By further dividing the number of larvae by an average figure for numbers of larvae per colony (i.e. average number of eggs per female); in this case 65; the following figure is obtained:

$$\frac{381}{65} = 5.9 \text{ adults per tree}$$

This is the estimate of the number of adults per tree necessary to produce the 14.3 percent defoliation that occurred in this stand. By dividing the number of adults per tree by the number of square feet in the cocooning universe (19.6 sq. ft. average), a gross estimate of the number of adults per square foot is possible.

$$\frac{5.9}{19.6} = 0.3 \text{ adults per square foot expected as compared}$$

with 0.28 adults per square foot actually recorded.

The compliance of calculated adult emergence per square foot with the observed emergence is much closer than one would expect in view of the large sampling errors involved and the gratuitous assumptions that were necessary in order to dismiss larval mortality from consideration. Even if the errors were considerably greater, however, the observed low adult emergence per square foot is not as surprising as it seemed at first glance. As a check on these figures, similar calculations were made for the other plots using foliage consumption figures per tree given in Table 4. These comparisons are presented in Table 13.

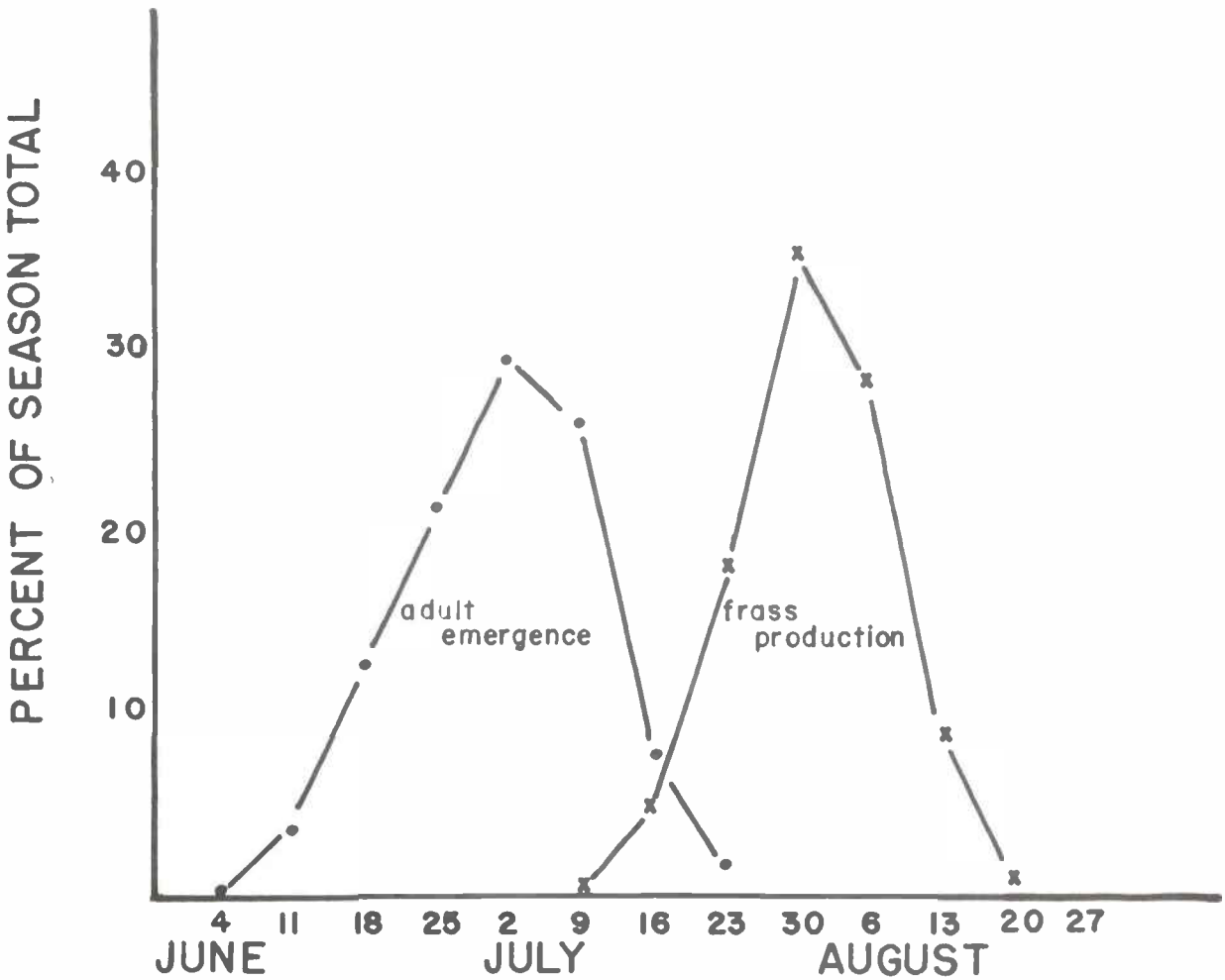
Table 13. Adult Emergence from Cages Compared with Number Expected on the Basis of Seasonal Frass Production

Plot	Emergence From Cages Adults Per Square Foot	Calculated Adults Per Square Foot	Difference (Actual Emergence minus Expected Emergence)
Beltrami	0.06	0.33	- 0.27
Cass	0.28	0.30	- 0.02
S. Cass	4.44	2.03	- 2.41
Portage	0.60	0.69	- 0.09

The differences between the observed and calculated adult emergence per square foot could be due to factors too numerous to mention. In passing, however, it is not surprising that over twice as many adults were recovered in the S. Cass cage (on a square foot basis) as were necessary for complete defoliation. Referring back to the section entitled "Natural Deterrents to Population Size" an example of over-population and its effects was cited. It follows that extremely favorable overwintering conditions, such as evidently were present in the S. Cass plot through 1949-1950, would make possible a 1950 population in excess of that necessary for complete defoliation. It would seem also that heavy populations at S. Cass in 1950 may have resulted in heavy mortality due to starvation or may subsequently result in lower fecundity in the surviving adults. The differences between observed and calculated emergence in the other plots might be due to any number of things; but sampling error could account for the whole amount.

To proceed with the subject matter of this section, it would seem that the emergence pattern from the S. Cass plot would be the only one of any value for comparison with seasonal frass production, i. e. progress of larval development. By plotting weekly emergence of adults (weekly emergence/seasonal total x 100) with weekly frass production (weekly frass/seasonal total x 100) the picture illustrated in Figure 18 is obtained.

Figure 18. 1950 adult emergence and frass production in percent of season's total.



There is a striking similarity in the shape of the two curves, suggesting that adult emergence is probably quite accurately reflected by the collections made from the single cage. The fact that the picture of adult emergence, although prolonged over a seven-week period, exhibits only one well defined peak, is of significance in control.

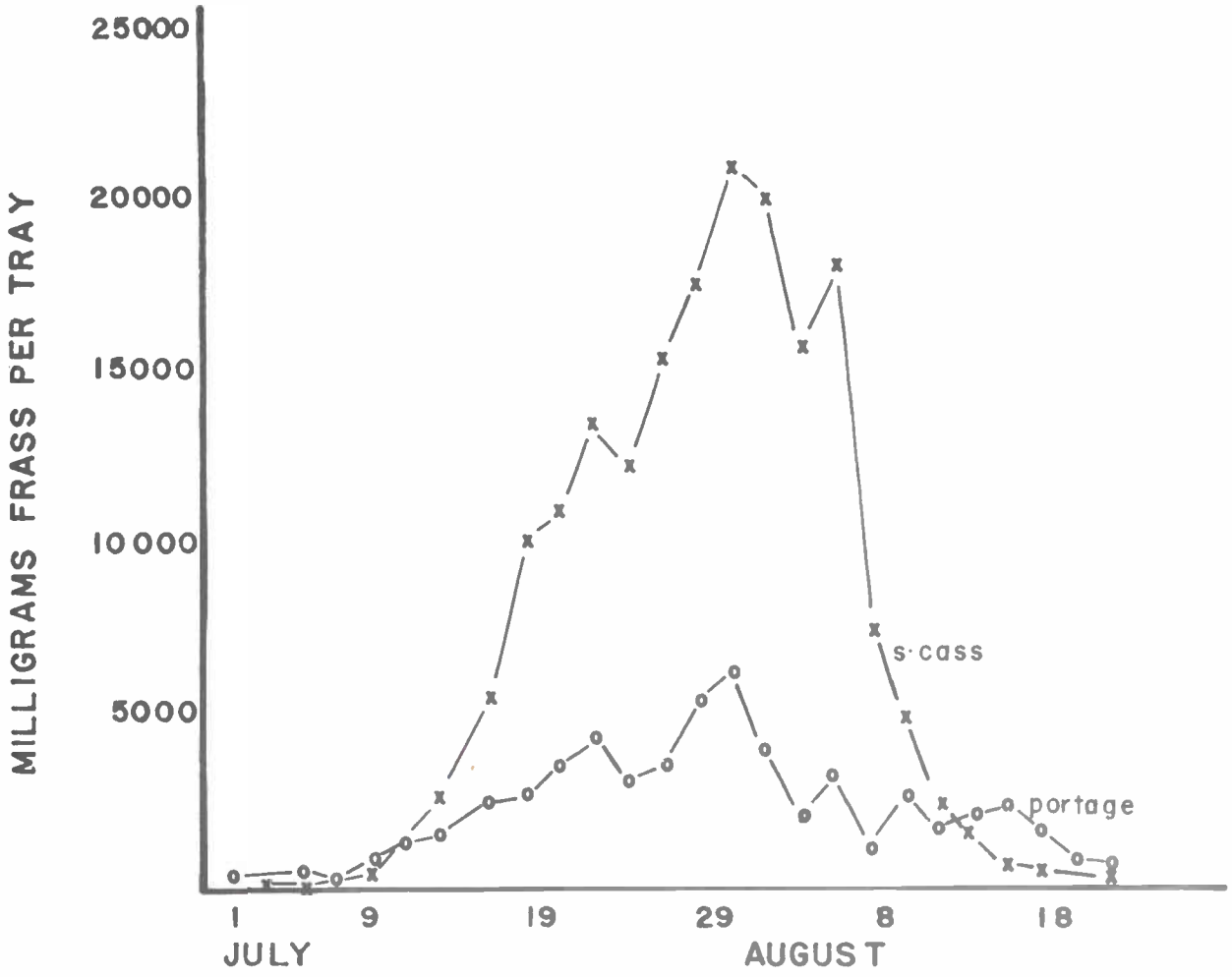
Duration of the Feeding Period in Five Study Plots

This problem was approached with the conviction that stand differences and their effects upon sawfly development probably would make area-wide estimates of spray timing impossible. To restate the problem: does seasonal distribution of adult emergence deviate from a normal curve (brought about by a dense canopy, high water levels or some other environmental factor) which make for significant local variations in the seasonal feeding curve? If it can be shown that such deviations do occur, and that they influence the form of the feeding curve, then the problem of direct control timing becomes exceedingly complex, if not impossible. If these deviations do not greatly influence the seasonal feeding pattern, then selection of a time for spray application can be made on a regional basis. The discussion that follows is an attempt to determine if this latter course is possible.

Site characteristics which can be considered of possible importance in retarding seasonal development of the sawfly are (1) degree of cocooning universe inundated and (2) density of canopy. If prolongation of the pre-pupal development period by submergence was to express itself in a later feeding peak than would be expected for a stand where the cocooning universe was not inundated, the 1950 feeding curve for Portage would seem the most likely place to look for such a phenomenon. By comparing the progress of feeding in this area and in the S. Cass plot particularly, the approximate degree of seasonal retardation due to inundation should be evident. An earlier discussion of the effects of prolonged immersion on cocoons at Portage (see Figure 9) was presented in the section of the paper entitled "Natural Deterrents to Population Size." Reference to Figure 6 will show that the quantity of the cocooning universe inundated at Portage through June was on the order of 80 - 95 percent; whereas inundation for the same period at Bena was 50 - 60 percent, for Baltrami it was 40 - 50 percent and for S. Cass less than 10 percent.

It has already been suggested on the basis of cocoon dissections made at Little Portage through July 22 that mortality of those larvae still in the ground increased sharply from the latter part of June through the first week of July. Incidence of the prepupa stage showed a concomitant decrease about this time for those above water and a similar decrease for those below water two weeks later. The fact that so high a percentage of those cocoons both under and above water after June 24 contained dead sawflies would indicate that release from immersion by the last week of June would not result in a substantially retarded larval feeding peak. By the same reasoning, a lower over-all larval population should have ensued. This is actually what seems to have happened in 1950 as Figure 19 would indicate. Here 48-hour frass production per 8 sq. ft. tray at Portage (average of 3) is plotted with 48-hour frass collections from S. Cass (also average of 3 trays).

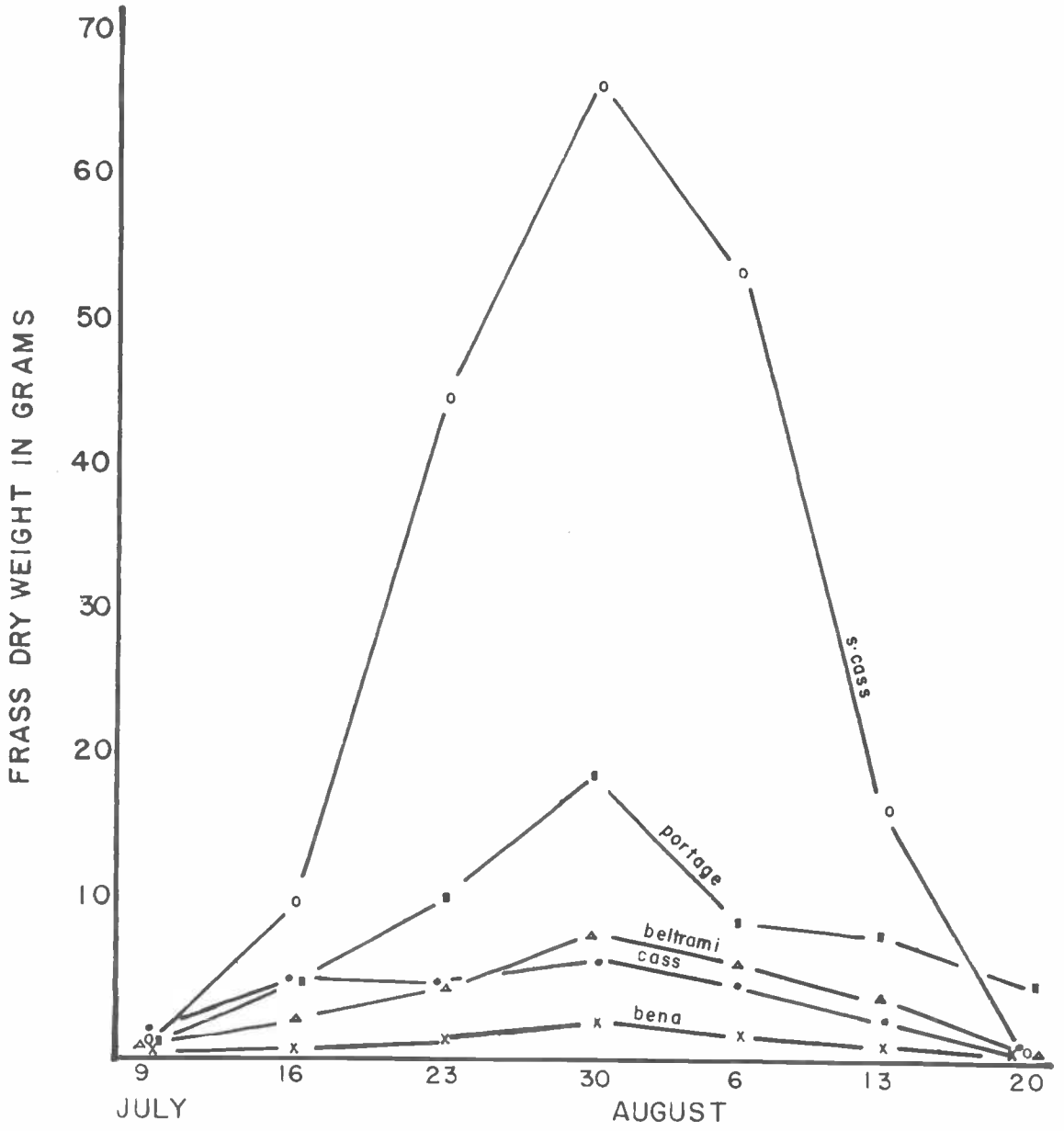
Figure 19. Frass collections for Portage and South Cass areas.



If anything, the larval population at Portage in 1949 had been greater than that at S. Cass. Both seemed relatively little influenced by the heavy rains that occurred at the time of cocooning in that year and which took such a toll of larvae at the Baltrami plot. There seems no question but that the mortality of over-wintering pre-pupae was a consequence of the unseasonable flooding at Portage caused by occlusion of the drainage outlet. Retarding the developmental period beyond the time when temperatures were optimum is the most logical explanation and one which is best reconciled with the evidence.

Just what was the extent of the retardation effect, if any, on those submerged cocoons which ultimately gave rise to adults? The best evidence would seem to be that derived from that portion of the S. Cass and Portage curves from August 11 through the 21. The Portage feeding was actually at a higher level through this period than was the S. Cass. How much of this is due to premature cessation of feeding resulting in exhaustion of the food supply at S. Cass is conjectural from the data offered in Figure 19; on the other hand, the composite curves shown for all plots in Figure 20 would indicate that Portage feeding dragged out perceptibly longer than the others. This figure indicates that there is a definite peak of feeding which coincides for all plots. This is contrary to expectations, but is of tremendous importance from the standpoint of control timing.

Figure 20. Frass production per week - all plots.



The picture just presented of feeding peak similarities in all plots in a large measure answers the question of whether or not delay in adult emergence is significantly affected by canopy density. The S. Cass plot, for example, a mixture of spruce, cedar and tamarack has a crown closure of 90 percent or more. The Portage stand on the other hand is closer to 65 percent closure. It is apparent from examination of the July 1 - 9 portion of the Portage and S. Cass feeding curves (Figure 19) that feeding took place somewhat earlier in the former than the latter. This can probably be traced to lower developmental temperatures during this period at the Cass plot, probably because of shading. This factor apparently was of no great importance in altering the shape of either curve. It raises the question, however, of the possible effect a large crown closure, i. e. lower soil temperatures, might have had in lowering mortality of those pre-pupae at Portage which were retarded by immersion and which subsequently died. This is but one of many potentially important influences which could prevent a catastrophe such as occurred in this plot in 1950. In regard to the percentage of the sawfly population which holds over in cocoons for two years and which as a consequence would not be vulnerable to a spray application the year following cocooning, complete information is not as yet available. Nine 3' x 3' cages are in place covering portions of the cocooning universe in which no 1950 cocooning took place. If any adults emerge from these cages in 1951 there will be no question but that they have held over from the 1949 season or earlier. It will be recalled that Graham (1928) found a very low percentage of holdovers (2 - 4 percent) in his cached material.

Field collections made in 1949 and 1950 after adult emergence was completed give reason to believe that the 2 - 4 percent figure is rather high. Better information on this subject will be available when the emergence from the above-mentioned cages is tabulated in 1951.

DIRECT CONTROL

Parasite Release

In 1950 the Dominion Parasite Laboratory at Belleville, Ontario generously contributed 10 colonies of the larch sawfly parasite, Mesoleius aulicus Grav. for release in Minnesota. Releases were made in 5 different tamarack bogs in the Cass Lake area upon arrival of the parasites at Cass Lake on July 16, four days after they were expressed from Belleville. The releases were made between the hours of 10 a.m. and 2 p.m. Conditions for release were very favorable, outdoor temperatures averaging approximately 75° F. with winds not exceeding 8 miles per hour. Following is a tabular summary of the operation:

Table 14. Location and Number of Mesoleius Adults Released at Cass Lake in 1950

Number of Colonies	Location	Total Parasites	Number of Living Parasites		
			Male	Female	Total
2	T146N-R31W-Sec.32 1/	1,000	334	438	772
2	T145N-R31W-Sec.28 2/	1,000	185	376	561
2	T144N-R31W-Sec. 4 3/	1,000	221	431	652
4	T143N-R32W-Sec.21 4/	2,000	507	877	1,384
Totals		5,000	1,247	2,122	3,369

1/ E and W sides of Hwy. 371 out of Cass Lake at Beltrami County Line.

2/ 1/2 mile S of entrance to Pike Bay Loop.

3/ E side Hwy. 371 at point 7 mi. S of Cass Lake.

4/ 3/4 mi. NE on Garfield Lake Rd. from Hwy. 65 - E side of road.

A follow-up on these releases was made in the fall of 1950 through dissection of cocoons collected at or near points of release in three of the four areas. The object of this work was to try to determine whether or not there was a noticeably higher percent of parasitization at the point of release than there was at points 2 or 5 chains removed. These data are expressed as percent parasitization - but each percentage figure is based upon only 50 cocoons. Since the degree of parasitism in all cases is so very small it would be unwise to attach much importance to the figures, but there may be some significance to the higher values at the points of release. The figures follow:

Table 15. Percentage Parasitisation of Larch Sawfly Cocoons at Various Distances from Point of Release

Location	Percent Cocoons Parasitized by Mesoleius				
	Point of Release	1 chain	2 chains 1/	3 chains 1/	5 chains 1/
T146N-R31W-Sec. 32	2	-	4 (W)	0 (W)	-
T144N-R31W-Sec. 28	16	-	8 (N) 12 (NE) 2 (SE) 2 (S)	-	-
2/ T143N-R32W-Sec. 21	0	-	0 (S) 0 (E)		2 (S) 4 (E)
2/ T143N-R32W-Sec. 21	12	-	18 (N) 6 (E)		6 (N) 2 (E)

1/ Letters designate direction of sampling spot from point of release.

2/ Same stand but points of release some 15 chains apart.

It was not practicable in 1950 to dissect large numbers of cocoons from the various check points described in Table 15. It was hoped, however, that the manner of sampling would yield information on the incidence of parasitism at the various distances from points where the parasites were released. If, in 1951, it becomes evident that parasitism is actually lower than these figures indicate, it seems likely that a measure of the parasitisation that actually took place at the time of release will be of value. There seems no doubt but that many larvae in the proximity of the release points were parasitised, and this knowledge can provide a basis for follow-up studies in subsequent years. These data are inserted here merely as a matter of permanent record.

Spray Timing Discussion

It was pointed out in the opening paragraph of this section that concern over the feasibility of reducing sawfly populations with one spray application was based on two things. One of these was the prolonged period during which oviposition took place, and the second was the ability of some larvae to remain in diapause so that development did not take place in one year. Each of these habits promised to make a portion of the population inaccessible to a single spray application. Because of the first of these, the manner in which the adult emergence and larval feeding curves coincided was of special interest.

Figure 21 illustrates the configuration of adult emergence and feeding curves for 1950. The curve for feeding is an average of all those from the 5 study plots expressed as percent of the aggregate frass production for all areas on a weekly basis. It will be recalled from Figure 20 that all of the infestations studied had their feeding peaks at the same time; so that the composite curve is an accurate record of feeding events for the Cass Lake region.

The adult emergence curve is based on the adults collected from S. Cass in one 3' x 3' cage. This is the best information available of cocooning under natural conditions. A curve for cocoons cached at the insectary (no canopy) reached a peak a week earlier on June 25, but on the other hand 9 out of 16 adults collected at Portage emerged on July 24, three weeks later than the S. Cass peak. If these extreme cases have any significance, however, they would certainly be reflected on the feeding curve. The coincidence of feeding peaks for all 5 plots must be interpreted as an accurate chronicle of feeding activity - i.e. establishment of colonies. In this connection it is of interest to note that sawflies allowed to reach the adult stage in early August (reared) did not oviposit in any shoots made available to them at that time. Some were caged on the most succulent shootsavailable, both in the laboratory and on trees growing outside the insectary; but no oviposition was observed. It is felt that possibly the shoots had hardened off sufficiently to make them unacceptable. Whatever the reason, there seems to be a factor or factors which operated in 1950 to equalize local variations in the adult emergence pattern so that ultimately feeding took place at about the same time in all stands examined.

The fact that there seems to be a normal curve of feeding which is not too different from one stand to another in a particular region would tend to remove a major obstacle to control. We can say with fair assurance that the adults which emerged at Portage on July 24 probably did not contribute greatly to the damage observed in 1950 because the height of feeding coincides with that observed at S. Cass. One has to assume then that the S. Cass curve of adult emergence, since it is the best available, is generally applicable throughout all plots.

Figure 21. Adult emergence and larval feeding of larch sawfly plotted with phenological observations.

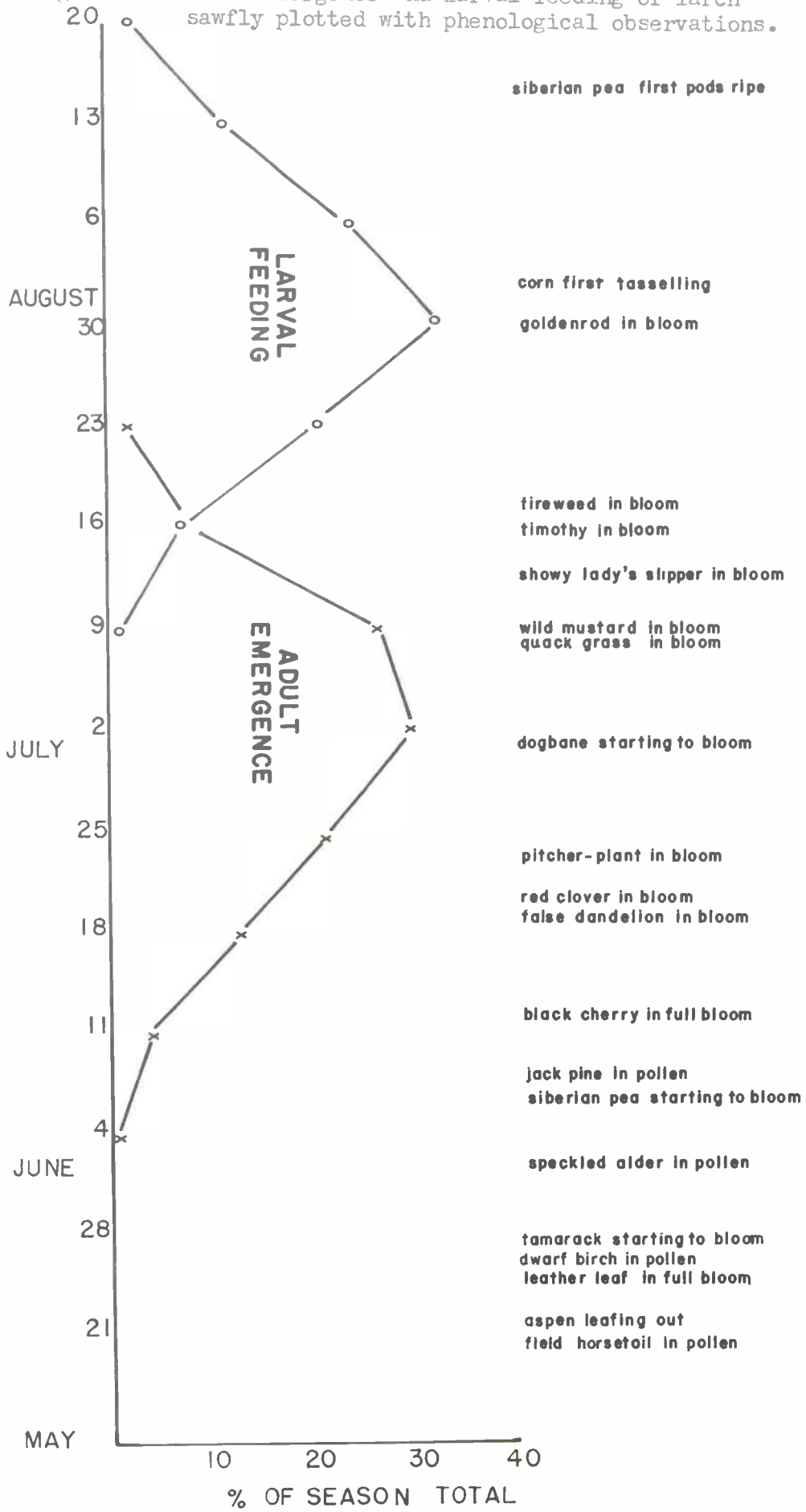


Figure 21 shows this curve and the composite feeding curve plotted simultaneously on a weekly basis. Note that the peak of feeding is one month from the date of the peak of adult emergence. In deciding when a spray application must be made, it should be remembered that some cocooning took place as early as July 9 in 1950, and in the absence of better information can be assumed to have progressed at an increasing rate to the point where the curve begins to drop. It would seem, therefore, that the best results would have been forthcoming in 1950 by spraying between the 16th and the 23rd of July. Those sawflies in the egg stage and in the first instar were observed to be relatively unaffected by the experimental spraying carried out in 1950, so that delaying as long as possible would be desirable. It is inevitable that a certain percentage of the population will be in the ground by this date; but by July 23 in 1950 this would have amounted to only about 10 percent of the total. It can be expected that between 20 - 50 percent of these would be killed by parasites, predators and adverse climate if the percentage of surviving cocoons on June 3, 1950 at Portage and Beltrami is indicative. These figures are based on 20 one square foot counts made at Beltrami and 7 one square foot counts at Portage.

Taking the S. Cass plot as an example, if the total number of larvae per square foot expected was reduced by 90 percent, we would have only 13.2 cocoons per square foot. Since the equivalent of 2.03 per square foot was considered sufficient for 100 percent defoliation of this stand in 1950 obviously there still would be a substantial population present in spite of the spraying, assuming that 100 percent mortality was achieved of all those insects present at the time of spraying.

When it is considered that this represents a substantial surplus over what is needed for complete defoliation the following year, adequate control would seem impossible. On the other hand, unfavorable temperature, parasitism that takes place in the larval stage and rodent predation would conceivably take a toll of overwintering pre-pupae which would be independent of cocoon density. Rodent predation is a possible exception, since fewer cocoons might possibly mean that searching by rodents would not be as efficient. There seems to be no alternative but to attempt control, however, in those cases where stands appear in danger of sustaining tree mortality.

Even as we concede that eradication of the sawfly is highly improbable, the protection aspect of insect control must be considered. This particular problem is not unlike some others, in that expenditure for control is limited by the value of the crop. Also, the biological characteristics of the insect make it possible that, in spite of spraying, the insect would still be present and potentially dangerous in succeeding years. What is even worse, the surviving population might be greater than if no spraying had been done. For, with a very high population, spraying might kill enough larvae to prevent exhaustion of the food supply and thereby permit more of them to complete their development than would have been able to do so had they all been permitted to feed extensively. This would not be true, however, if the 10 - 15 percent that cocooned prior to spraying sustained only light mortality due to natural control

factors; since this portion of the population would presumably have abundant food regardless of the total population present. In the case of the larch sawfly, one can justify a single spray application from a cost standpoint, and that perhaps only once every several years to forestall tree mortality. How, then, can even one spray application be justified when we have already conceded that it might protect the trees for only one growing season? As has been pointed out, tamarack is quite tolerant to defoliation and the sawfly is subject to a number of factors of natural control. Thus, if spraying will prevent defoliation of a stand in imminent danger of high mortality a degree of protection will be achieved, and if the surviving sawfly population is subject to heavy mortality from natural factors, spraying at the critical time could decide the fate of a particular stand. Further field investigations are necessary before one can establish the probability of any of the possible consequences of spraying just discussed.

The phenological observations made in 1950 are inserted adjacent to the dates on which these phenomena were observed. Although these represent data for only one year, they should prove of value in charting the progress of sawfly development in 1951. It is often impractical to determine time for spraying insecticides by using frass collections and adult emergence data from numerous plots, or to properly interpret such data in time to carry out necessary control action. It is felt that association of more easily observed events with peaks of sawfly oviposition and feeding will make it possible for timing of control measures to be handled more efficiently and more economically. Knowledge of occurrence of the phenomena described in Figure 21 is of particular value in that it permits anticipation of events in the sawfly developmental cycle.

Aerial Spraying Experiments

The difficulties incident to spraying for the larch sawfly are treated at considerable length in the section of this paper entitled "Seasonal Development and its Significance in Control." Aerial spraying of infested areas in 1949 with DDT at the rate of 1 pound per gallon of fuel oil per acre (Butcher, 1950) were encouraging enough to warrant additional experimentation in 1950.

In addition to spraying when late instar larvae were most abundant, as was done in 1949, it was considered desirable to spray several plots at the peak of oviposition. Accordingly, two areas known to be heavily infested in 1949 were selected for this latter work; one located near Ebro, Minnesota (T. 148, R. 31, Sec. 6 - 90 acres) and the other near Bagley, Minnesota at T. 147, R. 38, Sec. 29 - 80 acres. This spraying was carried out on June 30, 1950. From the best information available (see Figure 21) it would appear that the time selected for spraying was very close to the actual peak of adult emergence. This means that most of the immature sawflies were in the egg stage or the early larval instars.

Frass collections were made in each of the sprayed and in adjacent unsprayed check plots by means of collecting trays, 3' x 1' x 0.5'. Four of these trays were installed in each of the sprayed and in each of the check areas. The number used was, of course, too small to give a statistically reliable measure of the relative differences between the treated and the untreated areas. Experience has demonstrated, however, that while variation between such a limited number of collecting trays is likely to be considerable, nevertheless at high population levels gross differences such as might be expected between check and sprayed areas would be reflected, assuming that the spray application resulted in an appreciable population reduction. Frass collections were made at 7-day intervals subsequent to spraying in each of the check and sprayed areas and the volume of frass present in each tray was recorded in milliliters. The results of these collections are given in Table 16.

Table 16. Comparison of Frass Collections in Check and Sprayed Areas (Adult Spraying).

	Seasonal Average of 8 Trays (Ml.)	SD$\bar{X}$	SE$\bar{X}$
Sprayed	25.36	11.81	4.18
Check	38.62	12.55 *	4.44

* Difference in means on sprayed and check areas highly significant.

t = 3.492 5% level = 2.145

These figures indicate a 34.3% reduction in frass production based on the assumption that both check and sprayed areas had the same population before spraying. Since it was impossible to measure the respective populations prior to spraying it cannot be stated that they were in fact the same. At any rate the differences between the treated and untreated stands after spraying, while statistically significant, were of such a low order percentage-wise, that no recommendation for adult spraying can be made.

DDT in oil at the rate of 1 lb. per gallon per acre was applied to an 80-acre stand of tamarack on the Cass Lake Ranger District of the Chippewa National Forest at T. 146, R. 29, Sec. 28 in 1949 at the time when most of the larvae were in the late instars. Frass collections made in the check and the sprayed areas indicate that there was on the order of 81.2% more frass produced in the former than in the latter. In 1950, similar spraying was carried out in two blocks of heavily infested tamarack at Ely, Minnesota. The two blocks are located at

T. 62, R. 13 W., Sec. 3 (160-acres) and at T. 63, R. 13 W., Sec. 35 - 36 (56 acres). Four frass collection trays were installed in each of two sprayed areas and in each of two check areas. The insecticide was applied at the rate of 1 lb. DDT per gallon of fuel oil per acre as in 1949. Spraying took place in both areas on August 2nd. Reference to Figure 21 would indicate that the timing probably was such as to precede the peak of feeding. This is so because the seasonal progress of feeding was approximately 7 - 10 days later at Ely than it was on the Cass Lake District where the data comprising the curves for Figure 21 were obtained. Pursuant to the discussion of spray timing which is presented in the section entitled "Spray Timing Discussion" it is very likely that the timing coincided rather closely with the July 23 point on the larval feeding curve in Figure 21. This means that cocooning had taken place equivalent to 10 - 20% of the total. The results of the spraying are given in Table 17.

Table 17. Average Volume (ml.) of Frass per Tray in Sprayed and Check Areas.

	AUGUST			
	2	9	16	23
Check	9.3	82.1	35.3	5.0
Sprayed	6.8	20.5	3.8	0.1
Difference	2.5 1/	61.6 2/	31.5	4.9

1/ Difference between sprayed and unsprayed not significant.

2/ Difference between sprayed and unsprayed highly significant.

As the above data indicate, there was no significant difference in the sawfly population on the check and sprayed areas up to the time of spraying, which could be attributed to anything but sampling variation, on the basis of frass samples. One week later, however, there were statistically significant differences, indicating two populations with unequal means with the differences ostensibly due to spraying. Differences between the seasonal frass collections were also highly significant, and assuming similar populations in both check and sprayed plots prior to treatment, population reduction as derived from frass production figures was on the order of 77.3 percent in the sprayed area.

There seems little doubt but that the percentage figure just cited is representative of the degree of control that might be expected through application of insecticides to larch sawfly populations. Although data are not adequate to substantiate the phenomenon, it seems that the third to fifth instars are more readily affected by the toxicants than are the first two instars. Further work is needed to give weight to this belief, and also to determine the reasons for it. There is no opportunity at the present time to establish whether the earlier

instars are in fact more resistant to the insecticide or whether they escape contact more often by virtue of their more sedentary feeding tendencies.

It seems unlikely, when the prolonged oviposition and larval feeding periods are considered, that the timing of a single insecticide application can be improved upon. Those that cocoon early, that is before the time selected for spraying, must be considered invulnerable to the toxicant. Just wat the fate of this population residue was in 1950 will have to be determined in 1951 through cocoon and frass collections, in both the sprayed and unsprayed plots. A comparison of the two areas should yield better information on the net effect of the 1950 spraying.

SUMMARY

1. Field and insectary investigations on the larch sawfly, Pristiphora erichsonii Htg., were carried out in northern Minnesota from late May through August in 1950. The major objectives of this work were to (a) formulate a practicable approach to detecting sawfly damage, (b) develop methods for measuring the size of the sawfly population, (c) determine some of the natural control factors which contribute to fluctuation of sawfly populations (d) determine the association between tamarack decadence (terminal and radial increment reduction) and sawfly defoliation (deduced from oviposition injury), and (e) study seasonal development of the insect and evaluate its importance in the application of biological or chemical control measures.

2. Survey results in 1950 indicated that of 434,120 acres of tamarack type examined 224,521 acres sustained over 50 percent defoliation, 166,083 acres sustained a maximum of 15 percent defoliation and 43,516 acres showed less than 1 percent defoliation. These figures account for virtually all the infested tamarack in the Lake States through 1950.

3. Larch sawfly population studies in 1950 were largely confined to the collection and interpretation of larval frass in terms of numbers of larvae present. Frass collections were made during the course of larval feeding by the use of 8 square foot trays. It was found that the arbitrary number of trays used per stand was statistically a much less reliable indicator of larval abundance at low population densities than it was at high densities. As an aid to interpreting actual numbers of larvae present on the trees, an attempt was made to determine the dry weight of foliage consumed in relation to the dry weight of frass produced by each of the last four larval instars. A conversion factor was computed which permitted translation of frass dry weight obtained from field collections into quantity of foliage consumed on trees in a given stand, and from this the probable numbers of larvae present was estimated. The calculated quantities of foliage removed per tree were in good agreement with visual estimates of defoliation made in the same stands.

4. The possible effect of previous defoliation on the availability of oviposition sites in succeeding years was explored. It would appear that the amount of injury sustained through defoliation in any year can be estimated from the number of terminal shoots injured by oviposition, and, although the shoot injured by oviposition produces an abnormally short terminal or none at all the following year, the accumulative effect of oviposition and defoliation are manifested in a proportionate decrease in shoot length for the affected trees. It was found that a linear relationship obtained when percent of available shoots injured by oviposition in 1948 were plotted against average terminal shoot length in 1949. Measurements of terminal shoot length prevailing at the time of maximum oviposition in previously defoliated stands indicated that the terminal growth may be inadequate for establishment of large colonies of sawflies.

5. The percentage of the crown projection area containing surface water at the time larvae dropped to cocoon in 1950 was considered in the light of its possible influence upon larval survival. It was established that mortality due to drowning can be considerable (an estimated 57 percent of the total larvae present in one stand), but that this influence varies considerably from stand to stand.

6. Limited data make it appear that in a given situation retardation of development of overwintering pre-pupae through prolonged immersion may result in poor survival due to immersion itself, but when release from immersion occurs late in the spring the survivors may be forced to develop at higher than optimum temperatures. Because the larch sawfly has a low optimum temperature for development, high temperatures may have an additional adverse affect.

7. The need for early recognition of tamarack decadence and its possible use in anticipating tree mortality prompted a search for criteria which would be of value in setting up the need for control. It was found that there was good agreement between intensity of past defoliation (as evidenced by oviposition injury abundance) and tree vigor, as manifested in both reduced terminal shoot length and numbers of terminal shoots. There is also a suggestion that the relative size of needles from the various crown levels can be correlated with previous defoliation. More important, however, was the finding that in defoliated stands radial increment was reduced in proportion to reductions in shoot length and shoot number.

8. Seasonal frass collections in five dissimilar study plots demonstrated concurrent single peaks of larval abundance. Thus, adult emergence and oviposition did not produce variations in larval abundance in both space and time which would tend to make spray timing on an area-wide basis difficult.

9. Adult larch sawfly emergence took place over a seven-week period in 1950 with the peak occurring on July 2. The peak of larval feeding occurred on July 30, and feeding took place over a period of six weeks. The duration of both oviposition and larval feeding complicated the problem of direct control, since 10 to 15 percent of the larvae had already cocooned at the time optimum for controlling the majority of the population. Theoretically the 10 - 15 percent residual not susceptible to control would be sufficient to cause severe injury the succeed-

ing year.

10. The use of biological and chemical means for controlling the larch sawfly was investigated. Progress in biological control was limited to the release of a number of colonies of the parasite, Mesoleius aulicus Grav. which subsequently became successfully established near the point of release. Further tests with DDT oil sprays applied by airplane showed that they were relatively ineffective when used against the adult sawflies; but when applied to control 4th and 5th instar larvae the population was reduced by approximately 80 percent.

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